# THE HISTOLOGICAL STRUCTURE AND PHYSIOLOGICAL RESPONSE OF THE SENSORY UNITS IN THE KNEE-JOINT OF THE CAT

by

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'From a physiological point of view joints have been badly neglected'.

Gardner.

CONTENTS

# INTRODUCTION.

The capsules of mammalian synovial joints are known to contain a variety of sensory nerve-endings. Little is known, however, about the precise function of any of these nerve-endings. This is rather surprising, in view of the importance of the joints in health, and in view of the prevalence of diseases of the joints which are both crippling and painful. The appreciation of the relative positions of different parts of the body is exceedingly precise in man, even without the help of the eyes. For example, if the eyes are closed and a small object is put down with one hand it is possible, still with the eyes closed, to pick the object up again with either hand. Presumably the position of the hand is deduced from an assessment of the angles of the various joints. This implies that there must be available very accurate information about the relative positions of the bones forming each joint. Stopford (1921) concluded, from a study of human peripheral-nerve lesions, that, although information about movements of the fingers can be derived from endings in muscles and tendons, accurate localisation of the fingers depends on afferent impulses from the phalangeal joints.

Various physiological responses have from time to time been attributed to impulses in nerves from the joints. Comroe & Schmidt (1943), for example, described effects on respiration produced by passive movement of the limbs. They showed that changes in respiration could still be observed on moving the knee of the dog after cutting the tendons of surrounding muscles, and that the effect was abolished by denervating the knee-joint. The nerve-impulses producing the changes in respiration must therefore arise in the joint.

Impulses from nerve-endings in the joints have occasionally been observed, but the discharges have never been analysed in detail. Adrian and Umrath (1929) mentioned that they observed impulses in the sciatic nerve of a frog on movement of the knee-joint after all muscle branches of the nerve had been cut. Gardner, who has made an important contribution to our knowledge of the histology of the knee-joint of the cat, has also recorded an afferent discharge from the joint. He studied the innervation of the knee-joint (Gardner, 1944) and related the ranges of conduction-velocity for impulses in the articular nerves to the ranges of fibre-size in those nerves (Gardner, 1948b). In the course of this investigation he recorded afferent impulses in the posterior articular nerve, and observed

a spontaneous discharge whosefrequency could be increased by pressing lightly on the joint-capsule (Gardner,1948b).

This thesis reports the results of an attempt to record and analyse in detail the discharges produced in an articular nerve by deformation of the joint-capsule, and to locate and examine histologically the nerve-endings responsible for the various types of discharge. It was decided to use the posterior articular nerve to the knee-joint of the cat for the present investigation since Gardner used this nerve in his experiments, and most of the earlier histological work on the nerve-endings in joints was carried out on the capsule of the knee-joint of the cat.

The method employed for the demonstration of nerve-endings (gold chloride) is suitable for the impregnation of myelinated nerve-fibres and organised nerve-endings and it was with these that this investigation was concerned. Since it was found that one fibre of the posterior articular nerve supplied a number of individual nerve-endings a distinction between the morphological unit and the functional unit became necessary. The following terminology was therefore adopted and will be used throughout this thesis. Each individual organised nerve-ending is referred to as a 'receptor'. The group of receptors supplied by one fibre in the posterior articular nerve is referred to as

one 'sensory unit'.

It is appreciated that the joint-capsule may contain fine nerve-fibres which are not demonstrated with gold chloride, but it is considered unlikely that the discharges observed by Gardner, and those recorded during the present experiments, arose in such fine fibres.

The discharges from the joint observed by Gardner were complex and involved many units. It was therefore obvious that in order to analyse the response of any one sensory unit, a 'Single-fibre' technique would be required. In addition, since it was desired to observe the effect of various movements of the joint, the recording would have to be carried out in such a way that movement of the joint would not interfere. If more than one type of sensory unit were found in the joint, it would be necessary to dissect a unit from the joint-capsule, while recording its discharge, before the structure of the sensory units could be correlated with the types of discharge recorded from the articular nerve. The apparatus and techniques involved in these various procedures are described in Part I of this thesis. Part 2 contains the results of the analysis of the different types of response recorded from the articular nerve; the histological structure of the sensory units in the knee-joint is described in Part 3; and the correlation

of structure with response for each type of unit is given in Part 4.

All the work described in this thesis was carried out by myself, but much of the apparatus involved is the property of the Neurophysiological section of the Physiology Department of Glasgow University, for the assembly and construction of which Dr.T.D.M. Roberts and Mr.A.M. Andrew were responsible. Most of the apparatus is therefore not described in detail. The pieces of apparatus which are described more fully were wholly or partly constructed by myself, except where a specific acknowledgment is given.

The preliminary results of the analysis of the discharges in the articular nerve were presented in a communication to the Physiological Society in October 1952; more detailed results have since been published in the Journal of Physiology. A demonstration of the types of sensory unit in the knee-joint was given to the Physiological Society in June 1953, and a paper containing the results of Parts 3 and 4 is at present in the press.

This work was carried out during tenure of the M.M.I. Ure Research Scholarship, and, later, the Wm. Gardiner Research Scholarship, of the University of Glasgow.

# PART 1.

## METHODS.

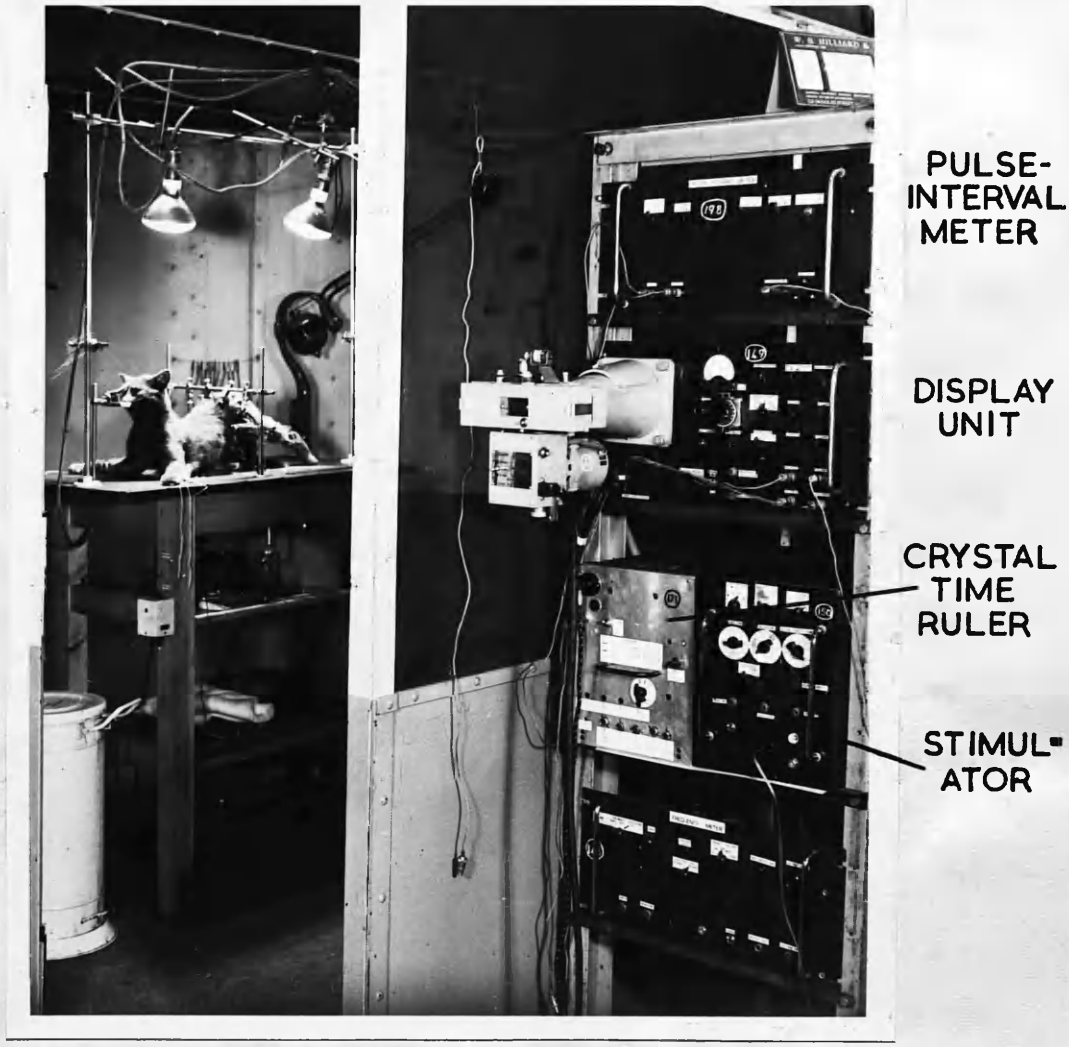



Fig. 1. General view of the apparatus employed. On the left is the screening cage doorway and through it the operating table can be seen; on the right is the display rack outside the cage.

## GENERAL LAY-OUT OF APPARATUS.

The experiments were carried out within a cage of wire netting of fine mesh, for screening purposes, and the general lay out of the apparatus is shown in Fig.1. The operating table and the experimental animal can be seen through the open door of the cage, and the rack containing the display unit and recording camera can be seen outside the cage. The power packs and most of the recording apparatus were kept outside the cage, while only the preamplifiers and those parts of the recording system which had to be visible, or which needed adjust-:ment, during the experiment were kept within the cage. Details of the apparatus are given at the appropriate places in the description of the experimental procedure.

## EXPERIMENTAL ANIMALS.

As has been mentioned already, the experimental animals used were decerebrate cats. Decerebration was carried out because the length of the experiments (up to 17 hours) meant that the animals had to be left unattended at intervals, and animals under an anaesthetic require continuous observation. In addition, the decerebrate preparation is thought to provide the nearest approxim-:ation to normal behaviour as far as sensory receptors

| Purpose for which used. | No. of animals |
|---|---|
| Analysis of discharges in the posterior articular nerve ..... | 28 |
| Histological examination of capsular tissue ..... | 1 |
| Analysis of discharges and histological examination ..... | 11 |
| Deaths during dissection ..... | 5 |
| No posterior articular nerve present ..... | 1 |
| Macroscopic dissection of the articular nerve only ..... | 1 |
| TOTAL | 47 |

Fig. 2. Classification of the experimental animals according to the purpose for which they were used.

are concerned. The total number of animals employed was 47. Five of these died before any experimental results were obtained, one was found to have no posterior articular nerve to either knee-joint arising in the usual position, and one was employed for tracing the distribution of the articular nerve in the capsule only. Of the other animals, some were used for the analysis of the responses of the sensory units only, one for histological examination of the knee-joint capsule only, and in the rest both analysis of responses and histological examination of the capsule were carried out. Fig. 2 shows the number of animals which were employed in each case.

Fig. 3. The apparatus used for the induction and maintenance of anaesthesia during decerebration.

## DECEREBRATION.

The technique of decerebration employed in these experiments was that of Dr.T.D.M. Roberts with certain modifications introduced by myself. Since this method is in some ways different from the procedure adopted by other workers, it will be described in some detail.

The animal was anaesthetised by the use of ether. Induction was carried out in a glass-sided chamber, to which ether was delivered from a wash bottle by bubbling air through ether in the bottle by a hand bellows (Fig.3). The animal could be observed through the glass sides of the box and when the breathing was deep and regular, and no active movements were made if the box was tilted, ether was dripped onto the toe of a woollen sock and this was pulled over the cat's face as an anaesthetic mask. The animal was carried to the operating table and tied down on its back by strings attached to the limbs. Ether was dripped onto the sock as required to maintain a satisfactory level of anaesthesia.

The fur on the neck from jaw to sternum was removed with scissors, and an incision made through the skin from the suprasternal notch up to the hyoid bone. The skin flaps were dissected free of the underlying tissue and held aside with clip weights. The muscles along the midline were separated to expose the trachea, care being taken not to damage the vein which lies ventrad to the

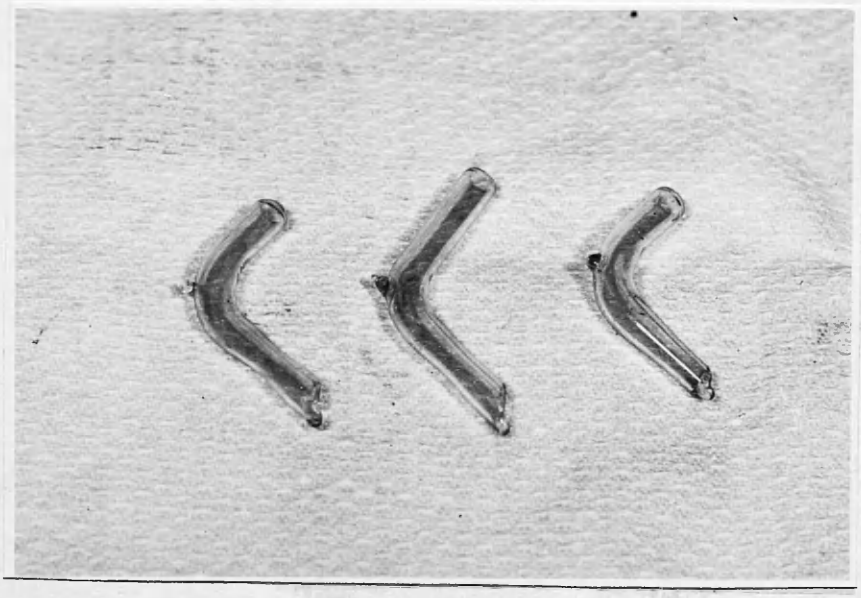


Fig. 4. The type of tracheal cannula employed.

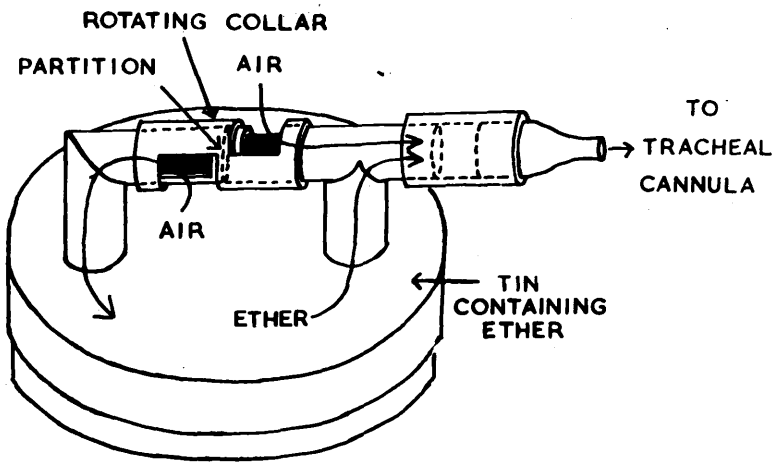



Fig. 5. Diagram of the anaesthetic tin used to maintain a steady level of anaesthesia. By rotating the collar the proportion of ether to oxygen in the inspired air can be adjusted.

trachea. The sides of the trachea were cleared by blunt dissection and a linen thread passed round it using an aneurysm needle. The thread was then tied in a half knot round the trachea. The trachea was raised by the thread and a cut made halfway through it between two tracheal rings craniad to the thread. The edge of the cut was gripped in small Spencer-Wells forceps and a tracheal cannula of suitable size was slipped into the trachea and fixed in position with the thread. The type of cannula used, designed by Dr.T.D.M. Roberts, is shown in fig.4; it consisted of a piece of glass tubing curved as shown, with one end bevelled, and a small glass projection on it to which the thread could be tied to prevent the cannula slipping out of the trachea. The cannula was then connected to an anaesthetic tin by a short piece of rubber tubing. The anaesthetic tin, designed by Dr.T.D.M. Roberts, is shown diagramatically in fig.5. The inspired air passed directly into the tracheal cannula through one aperture in the sleeve, and indirectly via the other aperture in the sleeve and the tin, which contained a pad soaked in ether. An air-ether mixture was thus obtained, and the proportion of air to ether could be altered by rotating the sleeve. An essential of such an apparatus is to have very little

'dead-space' between lungs and atmosphere; this was achieved by making the various pieces of tubing as short as possible. The proportion of air to ether required to maintain steady anaesthesia varied from animal to animal but it usually proved satisfactory to commence with equal parts of ether and air, and then adjust slightly later if required. If at any stage during the decerebration the animal became too deeply anaesthetised and the breathing ceased, artificial respiration was applied by connecting a T-tube to the cannula and gently blowing expired air into one limb of the T-tube, via a piece of rubber tubing, while closing the other limb of the tube at intervals with the finger. If at this or any subsequent stage of the experiment the heart stopped, artificial pumping of the heart was carried out by making an incision in the abdominal wall, inserting a finger through it and pumping the heart by applying pressure through the diaphragm, while continuing the artificial respiration. If this was unsuccessful, the tracheal cannula was connected to a respiratory pump, and the chest wall opened. The heart could then be mechanically pumped until it resumed its normal rhythm. Artificial respiration with the pump had then, of course, to be continued throughout the experiment. On one occasion the heart recommenced to

beat after almost 30 minutes of manual pumping, and the experiment was successfully completed. Trouble with the respiration occurred in few cases, so that these procedures were rarely necessary.

After steady anaesthesia with the anaesthetic tin was obtained, the sterno-mastoid and sterno-hyoid muscles were separated by blunt dissection until the carotid artery was visible. This was separated for about 3 cm from the accompanying vagus and other nerves by careful blunt dissection. The artery was then tied off with thread. This procedure was repeated with the other carotid artery, and the incision in the neck sewn up round the tracheal cannula. The head was then fixed in the Roberts (1951) head-holder, the anaesthetic tin was disconnected, the animal was turned over, the head-holder fixed in a bosshead so that the head was about 8 inches above the table, and the anaesthetic tin was reconnected. The tin had to be supported on wooden blocks so that kinking of the trachea was avoided.

Steady anaesthesia was essential before the next steps could be taken. An incision was made in the scalp from the root of the nose well down onto the back of the neck. Both skin flaps were held aside with clip weights. The fascia over the origin of the right

temporal muscle was cut through with a scalpel, and the muscle was scraped cleanly from the bone using the handle of the scalpel. The mass of muscle was cut away leaving about ½ cm at each end where there were large vessels. With a trephine about 1 cm in diameter a hole was made in the most prominent portion of the parietal bone about 1½ cm from the midline. The disc of bone was removed. Pressure applied to the vertebral arteries close behind the wings of the atlas caused the dura in the trephine hole to sink inwards. With bone-nibbling forceps the area of the trephine hole was doubled caudad and ventrad care being taken not to cut the dura. It was usually possible to do this without maintaining the pressure on the vertebral arteries. The hole was made large enough to comfortably admit the little finger. The edges of the hole were sealed with bone wax to stop any bleeding from the cancellous bone, and to reduce the risk of aspiration of air and resultant air embolism should the blood pressure fall later in the experiment. After closing the vertebral arteries as described above, an incision was made in the dura and a small portion of brain was scooped out using a decerebrating spoon. The occipital lobe of the exposed hemisphere was then turned forward revealing the corpora quadrigemina. With the spoon a cut was made (forwards and downwards) through the

mid-brain between the colliculi. All the brain rostrad to the section was then scooped out, and the cavity mopped out with cotton wool swabs. In the initial experiments the vertebral arteries were held until there was no further bleeding on relaxing the pressure. This often required the application of considerable pressure on the vertebral arteries for some time, which was not only very tiring to the hand, but reduced the blood supply to the respiratory centre so that the respiration sometimes ceased, with the ensuing complications. Most of the bleeding within the skull was noted to come from the region of the sella turcica. The following procedure was therefore adopted. Having mopped out the skull as described, while maintaining the pressure on the vertebral arteries, several small pieces of 'Gel-foam' were placed in the region of the sella turcica, covered with a small pad of cotton wool, and firm pressure on this pad downwards and forwards was applied with the little finger. Pressure on the arteries could then be relaxed, the blood supply to the midbrain remained unimpaired, and the pressure on the cotton wool could be maintained without much effort until there was no further bleeding on removing the finger. The skull was then loosely packed with cotton wool and the skin incision

sewn up. This procedure was found to produce the minimum of shock, and was adopted in all but the preliminary experimants.

## THE DISSECTION OF THE POSTERIOR ARTICULAR NERVE.

Since it was required to move the hind limb passively, it was obviously desirable to abolish any decerebrate rigidity present in the muscles, and to limit as far as possible any twitching of the limb. This was carried out by denervating the limb. As it was found simpler for a right-handed person to carry out the later stages of the dissection on the left hind limb than on the right, the left leg was used in all but the first few experiments and the procedure now described applies to dissection of the left hind limb. The fur was removed from a small area of skin in the left groin overlying the femoral vessels. An incision was made in this position and the femoral nerve located where it passed beneath the inguinal ligament. It was separated from a small vessel which usually accompanied it and the nerve was cut through. By pulling the medial skin flap towards the midline, it was possible to see the obturator nerve in part of its course lying on top of adductor femoris and dipping beneath the gracilis muscle. It was also sectioned, and the incision was sewn up. The sectioning of the femoral and obturator nerves was usually carried out after the tracheal cannula had been inserted, and before the decerebration was completed. This made turning the animal onto its back for a second time unnecessary. The

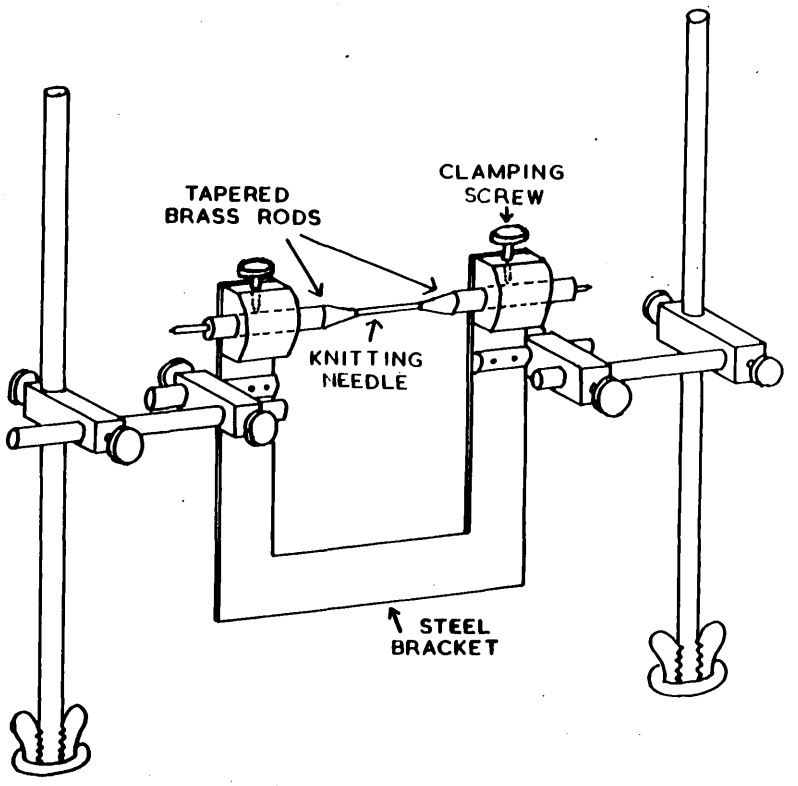



Fig. 6. Diagram of the type of spinal clamp found to be most effective. The knitting needle is inserted through the muscles of the back just dorsal to the vertebral column; the tapered rods are then pushed against the animal and fixed with the clamping screws.

fur was removed from the whole of the posterior aspect of the limb and the animal fixed in a spinal clamp with its back uppermost. Several types of spinal damp were employed, but the most satisfactory type is shown in fig.6. It consisted of a U-shaped steel frame with rods attached which could be fixed in bossheads on uprights clamped to the operating table, making the frame rigid. The frame carried two short tapered brass rods which could be moved horizontally and clamped in any position. Each of these rods was drilled so that a small metal knitting needle would pass through both of them as shown. The needle was pushed through the muscles of the cat's back just above the spine and forward of the pelvis, and the ends of the needle inserted in the rods, which were pushed towards the animal until the muscles were gripped firmly, and the rods were then clamped in that position. This type of clamp prevented forward or sideways movement of the spine and pelvis, although some rotation about the needle could take place. It proved more satisfactory than other forms of clamp which gripped the animal's spine or pelvis from the outside.

A small incision was then made in the skin in the groove between the head of the femur and the greater trochanter, the underlying muscle was split and the sciatic nerve was then

Fig. 7. The appearance of the preparation immediately prior to the commencement of the dissection of the posterior articular nerve. The animal is fixed in the spinal clamp; the femur has been made rigid by the insertion of bone-pins into the greater trochanter and the femoral condyles, the pins being fixed in clamps, and the fur has been removed from the back of the leg.

visible in the groove. The nerve was cut through, care being taken not to cut a small vessel which was often bound to it by connective tissue. The limb was now almost completely denervated and the muscles, with the exception of the sartorius, relaxed. Even though this latter muscle was not denervated, it did not seriously impede passive flexion of the knee. A bone-pin was then inserted in the greater trochanter, through the incision made when sectioning the sciatic nerve. This incision was then sewn up. A second bone-pin was inserted into the femoral condyles, so that it projected horizontally from their external aspect. These two bone-pins were fixed in a system of rods and clamps so that the femur was rigidly held, but the tibia could be freely flexed on the femur in such a way that when the tibia was horizontal it made an angle of about 140 degrees with the femur. A third bone-pin was inserted in the tibia about one inch above the ankle-joint, so that when the limb was flexed or extended this pin remained approximately horizontal; it served as a pointer to indicate the position of the tibia relative to the femur. The appearance was now as is shown in fig.7.

A longitudinal skin incision was then made down the back of the leg from the level of the greater trochanter to the ankle. The skin flaps were freed from the

underlying tissues and held aside with clip weights. Care was taken not to damage the large vein traversing the whole length of the back of the leg; this vein was left attached to the lateral flap and was turned aside with it. The popliteal fat pad was then separated from the gracilis muscle, and the connective tissue sheath of the gastrocnemius muscle was slit down to the ankle. On pulling the fat pad laterally two, or sometimes three, vessels could be seen running from the fat pad into the gracilis muscle. These were cut between double ligatures. Several vessels from the fat pad to the gastrocnemius were now visible. Those to the medial head, usually two in number, were cut between double ligatures. The sciatic nerve and its branches to the gastrocnemius muscle could now be seen in the popliteal fossa. The vein running from the ankle to the fat pad on the surface of the lateral head of gastrocnemius was ligatured at the ankle and as it entered the fat, and the intervening portion removed. The large vessels connecting the fat pad to the popliteal vessels were then cut between double ligatures and the pad turned medially. Several vessels from the pad to the biceps muscle could now be seen; these were ligatured as with

the others, and the fat pad was then completely removed.

The two heads of the gastrocnemius muscle were separated from above downwards, the tendon of the medial head was cut and pulled medially, and the medial head was separated from its attachments all the way from its insertion to its origin. During this process vessels connecting the muscle with the posterior tibial vessels and the back of the knee-joint were cut between double ligatures. The nerve to the medial head was then cut and the main branches from the popliteal vessels to the muscle, which entered it from above, were ligatured. The origin of the medial head was then cut through and the muscle was removed completely. The medial popliteal nerve, its continuation as the posterior tibial nerve, and its branches were not damaged by this procedure as they were firmly bound by connective tissue to the lateral head of the gastrocnemius. By pulling the lateral head further laterally, it was now possible to see these nerves lying on the surface of this muscle. The first branches of the posterior tibial nerve constitute the leash to the posterior tibial muscles. The first nerve of this leash is a small branch which travels with the leash in the first part of its course, and then leaves it to pursue a rather tortuous course to the back of the knee-joint.

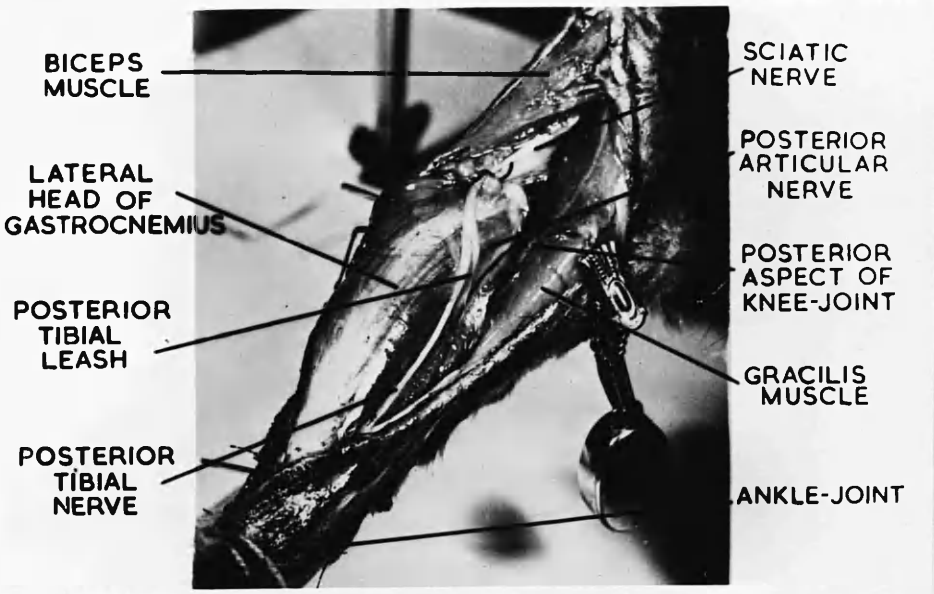



Fig. 8. The appearance of the preparation after removal of the medial head of the gastrocnemius muscle. The medial popliteal nerve, and its continuation as the posterior tibial nerve, can be seen running across the surface of the lateral head of gastrocnemius which has been pulled laterally. The posterior articular nerve is just visible as it leaves the leash of nerves to the posterior tibial muscles to run towards the back of the knee-joint.

This nerve is the posterior articular nerve to the knee-joint. The dissection at this stage is as in fig.8, where the articular nerve is just visible as indicated.

All exposed muscles and nerves were then coated with warm liquid paraffin to prevent drying. The connective tissue ensheathing the posterior tibial nerve was slit and the nerve was cut about an inch distal to the point of origin of the posterior tibial leash of nerves; the branches of the leash were also cut where they entered the various muscles, so that the posterior articular nerve was the only branch left intact. Forceps were attached to the proximal end of the cut posterior tibial nerve, and allowed to hang so that traction was applied to the nerve but not to its articular branch. The articular nerve was then dissected off the back of the posterior tibial nerve until about 3 cm of nerve was obtained. The mode of origin of the articular nerve is quite characteristic and makes this dissection possible. Whereas the other branches leave the main trunk shortly after issuing from the nerve-sheath, the articular nerve runs down the deep aspect of the posterior tibial nerve, after leaving the main sheath, for a variable distance during which it is bound to the nerve by connective tissue. The length of this portion of the nerve varied from animal

to animal, and so, therefore, did the total length of articular nerve available for the experiment. It was important to obtain as much of the nerve as possible since on this depended the distance of the recording electrodes from the joint, and hence the degree of movement of the joint obtainable without interfering with the electrodes. The articular nerve was therefore dissected free from the posterior tibial nerve until its actual point of origin from this nerve (or its continuation as the medial popliteal nerve) was reached. It was cut here, the end gripped in fine forceps, and it was dissected free from the lateral head of gastrocnemius and turned across the posterior tibial vessels so that it lay on the surface of the posterior tibial muscles. This part of the dissection had to be carried out with the utmost care using very fine scalpels and keeping the nerve coated with liquid paraffin, for it proved easy to damage the nerve by excessive traction, kinking or drying.

The lateral head of gastrocnemius was then again pulled laterally and all the vessels supplying it from underneath were tied between double ligatures. These vessels were variable in position, but usually consisted of one at the ankle, one halfway along its length, and one near its origin. Special care had to be taken when ligaturing this latter vessel not to include in the

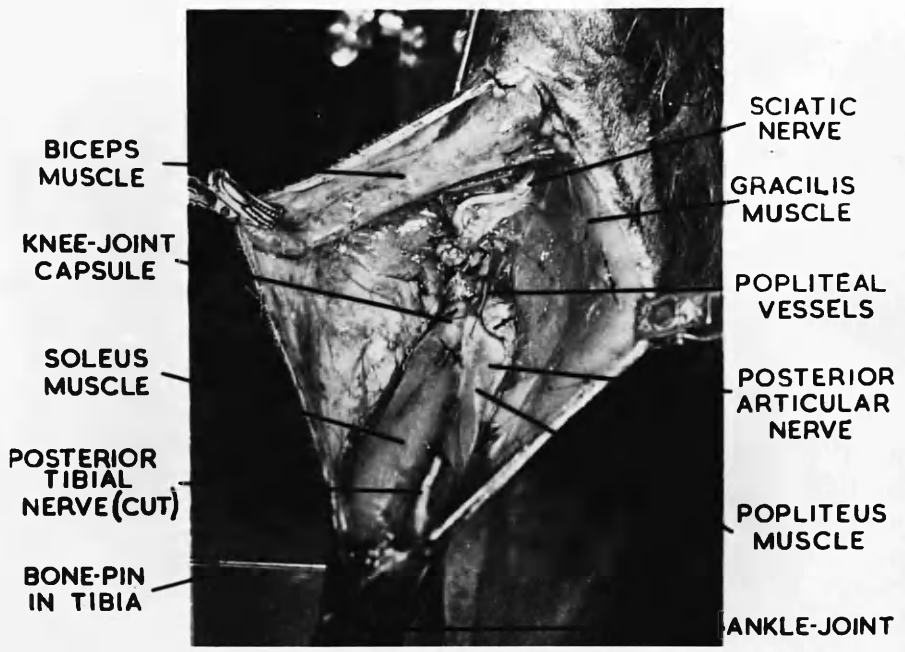



Fig. 9. The appearance of the preparation after the removal of the lateral head of gastrocnemius. The back of the knee-joint is now exposed; the articular nerve has been cut at its point of origin from the posterior tibial nerve, and lies coiled on the popliteus muscle.

ligature the articular nerve as it entered the knee-joint. This was accidentally done on one occasion, so that no experiment on that limb was possible. The tendon of the lateral head of gastrocnemius was then cut at the ankle and the muscle was dissected free from below upwards. The main vessels supplying it from above, and two small branches from the side of the knee-joint had to be ligatured in the process and the lateral popliteal nerve had to be cut. The origin of the muscle was then cut through and it was removed completely. The back of the knee-joint was then fully exposed (fig.9). The skin flaps were then pulled aside and fixed so as to form a pool, which was filled with liquid paraffin.

Throughout the dissection great care was taken that no bleeding took place - hence the use of double ligatures on all occasions. Any accumulation of blood over the knee-joint capsule made accurate localisation of sensory units impossible, even after attempts to remove any clot which had formed. This meant that the further dissection necessary for the experiments in Part 4 was impossible.

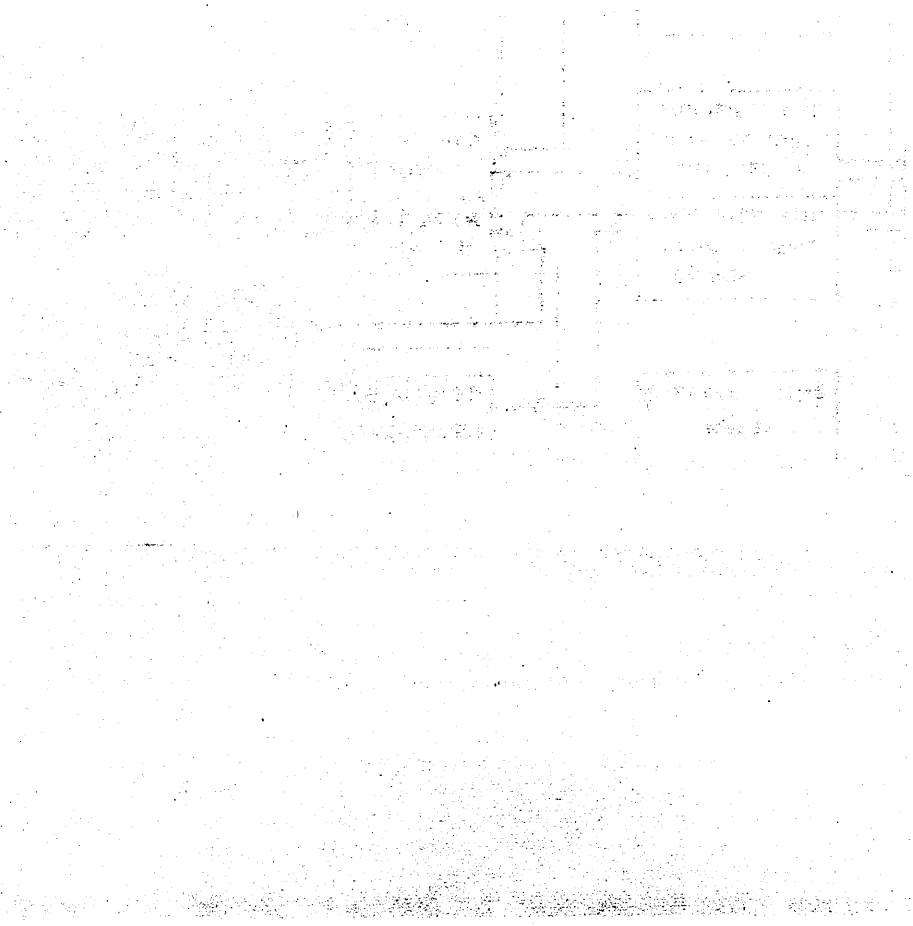
The decerebration and the dissection of the posterior articular nerve took between 3 and 4 hours on each occasion.

## TEMPERATURE CONTROL.

Since the decerebrate preparation could not control its own temperature, it was necessary to prevent a steady fall in the body temperature of the animal by supplying heat externally. This was done by having the operating table warmed by electric light bulbs beneath it, controlled by a Simmerstat, while heat was supplied from above by two infra-red lamps mounted on a frame as shown in Fig.1. It was soon found that the frequency of the impulses recorded from the articular nerve was altered by changes in the temperature of the paraffin pool. It was therefore necessary that the temperature of the pool be accurately controlled, and this was accomplished by using a thermal control unit, regulated by a thermistor dipping into the paraffin of the pool. By directing the lamps towards the pool, the temperature of the paraffin could be maintained at any desired level, and the heat supplied to the animal at the same time was just sufficient to maintain its body temperature within a few degrees of normal. The pool was usually kept at 37°C with a possible variation of about ±1 degree.

The thermistor was fixed in such a position that its tip was close to the articular nerve beneath the surface of the pool even when flexion or extension was

carried out, and so that it did not interfere with movement of the joint.



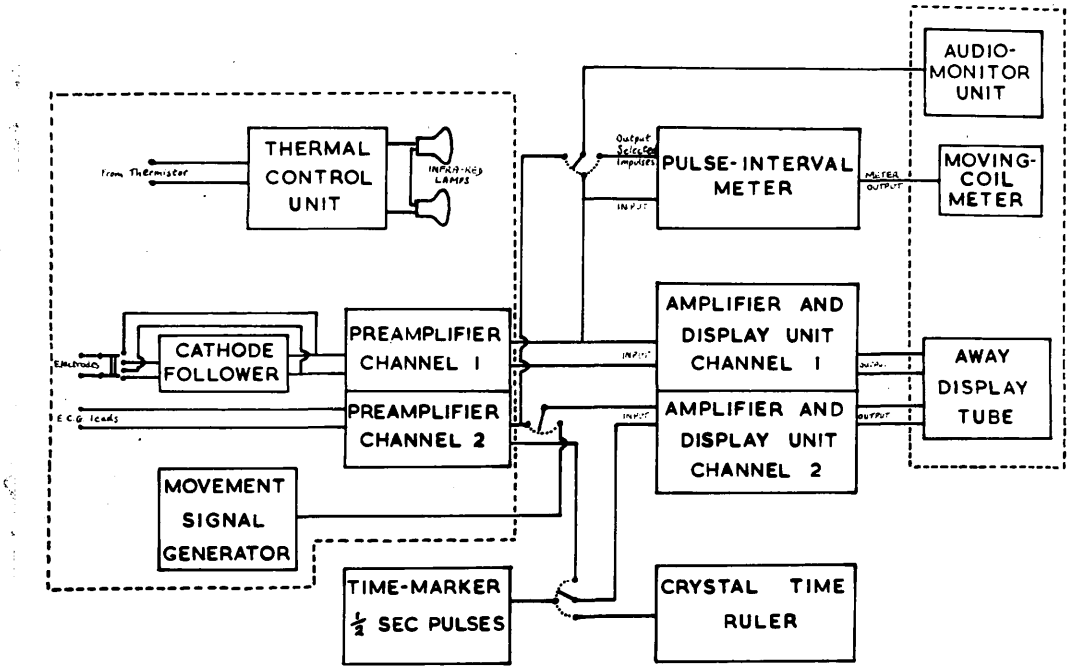



Fig. 10. Block diagram of the recording apparatus. The pieces of apparatus within the dotted lines are mounted inside the screening cage; the rest of the apparatus is outside the cage.

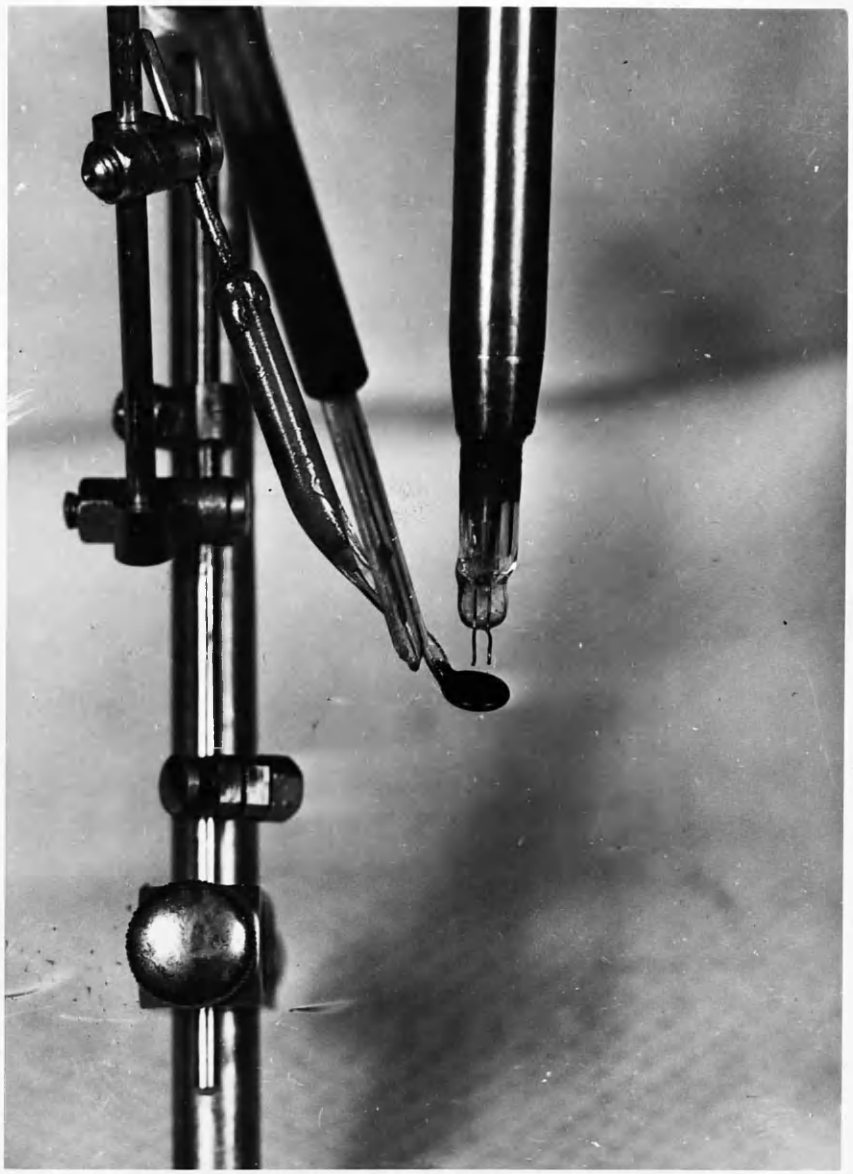


Fig. 11. Photograph of the thermistor, black glass platform and recording electrodes in the relative positions they occupy when immersed in the paraffin pool over the back of the knee-joint.

Fig. 12. The cathode follower. The input sockets can be seen on the front, the power cable lies on the left, and the lead to the preamplifier on the right.

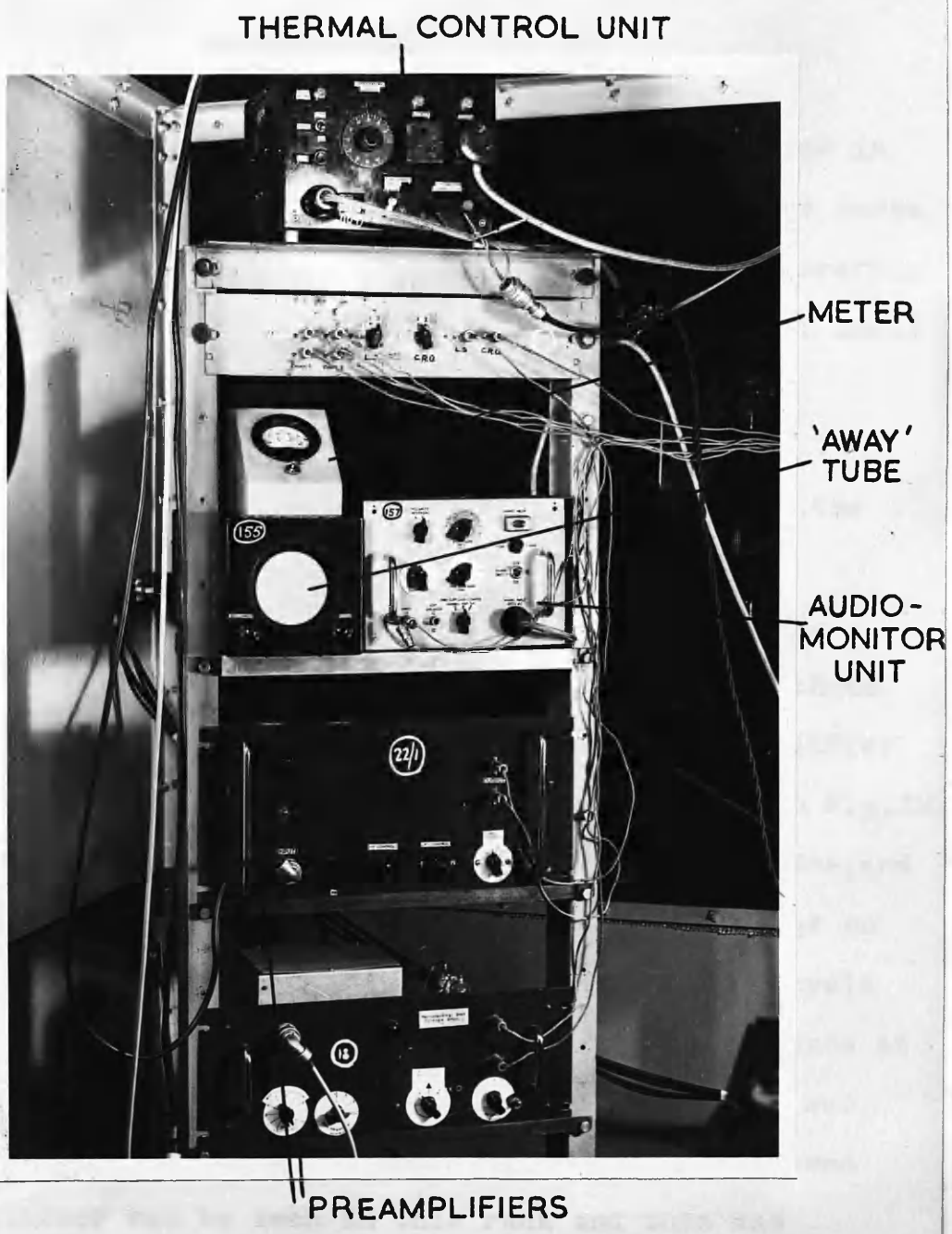



Fig. 13. The display rack within the cage containing the pre-amplifiers, the audiomonitor unit, the 'away' oscilloscope tube, and the moving-coil meter giving the frequency of the impulses. The thermal control unit stands on top of the rack.

## THE RECORDING APPARATUS.

Fig.10 is a block diagram of the apparatus used in recording the discharges in the posterior articular nerve. The electrodes dipped beneath the surface of the paraffin in the pool over the knee-joint. They consisted of small hooks of platinum wire sealed into glass which was enclosed in a brass tube, connected to earth, the electrodes and leads being thus screened almost to the tip, (fig.11). Wander plugs were fitted to the electrode leads so that the leads were as short as possible, and the plugs could be connected to a cathode follower, or connected direct to leads to a preamplifier within the cage. The cathode follower is shown in Fig.12. It could be fixed in position close to the electrodes,and was introduced into the circuit when the nerve-twigs on the electrodes were so small that considerable 50 cycle interference was encountered due to the high impedance at the electrodes. The balanced input pre-amplifier was mounted in a rack within the cage, (fig.13). A second preamplifier can be seen in this rack and this was sometimes used for amplifying the potentials of the electrocardiogram picked up by two leads connected to fore and hind limbs, or head and hind limb, of the animal. The output from this amplifier could be fed

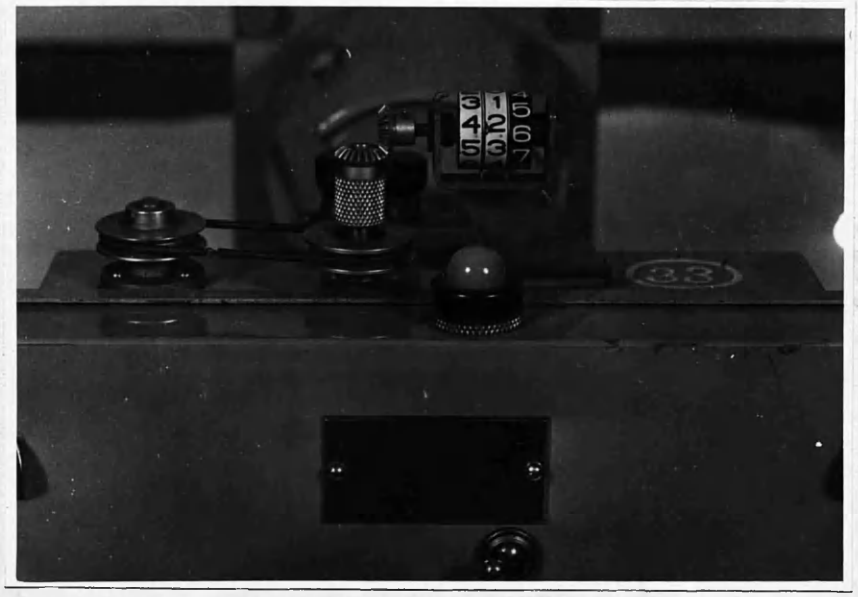



Fig. 14. The footage indicator geared to the spindle of the oscilloscope camera.

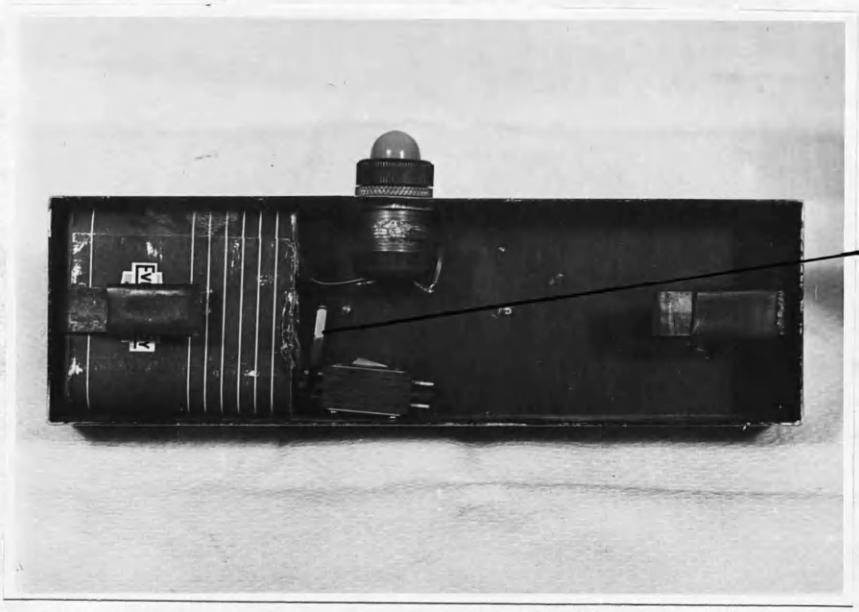



Fig. 15. The arrangement for indicating when the recording film runs out. The spring contact rests on the recording paper and when this runs out, the contact touches the camera case and completes a circuit through battery, switch and warning lamp.

into the audiomonitor unit, shown above in fig.13, so that the heart beats were audible. This was useful during the dissection as any change in heart rate was immediately noticeable.

The two preamplifiers were connected, via further amplifiers of conventional design, to a double beam display unit in the rack (which is shown in fig.1), outside the cage. A Cossor camera was mounted in front of the oscilloscope tube. Since it was found useful to know how much film had been used at any point, a footage indicator was geared to the driving spindle of the camera (fig.14). A pilot light was also fitted into the camera lid so that when the film ran out a circuit through the lamp, a battery and a switch was completed and the warning light then showed. The arrangement is shown in fig.15.

After a number of experiments had been carried out, it became obvious that an instrument which would give a direct reading of the value of the impulse-frequency, when recording from a 'single-fibre' preparation, would be of great value. The usual type of frequency-meter such as that shown at the foot of the display rack in fig.1, had the disadvantage that there was a certain time lag before the true frequency was recorded, and peak values were not

accurately registered at all. An instrument was therefore designed which, by measuring the interval between consecutive impulses and producing a voltage output proportional to the reciprocal of this, could be made to record, on a calibrated moving coil meter, the instantaneous frequency of the impulses. This instrument has been described elsewhere (Andrew & Roberts, 1954). It is shown at the top of the display rack in fig.1 and its input was derived from the first preamplifier described above. This pulse-interval meter had an adjustable trigger level so that it was possible to select, for counting, the peaks of the action-potentials of one unit although other units of smaller amplitude were present in the discharge recorded from the articular nerve-twig.

Two forms of time marking were used in these experiments. The output from either the crystal time ruler, also contained in the display rack in fig.1, or from a clockwork system giving $\frac{1}{2}$ sec pulses, was connected to the second beam of the oscilloscope in addition to the e.c.g. signal or movement signal (see later).

It was necessary to be able to see the oscilloscope tube, to observe the impulse-frequency, and to adjust the

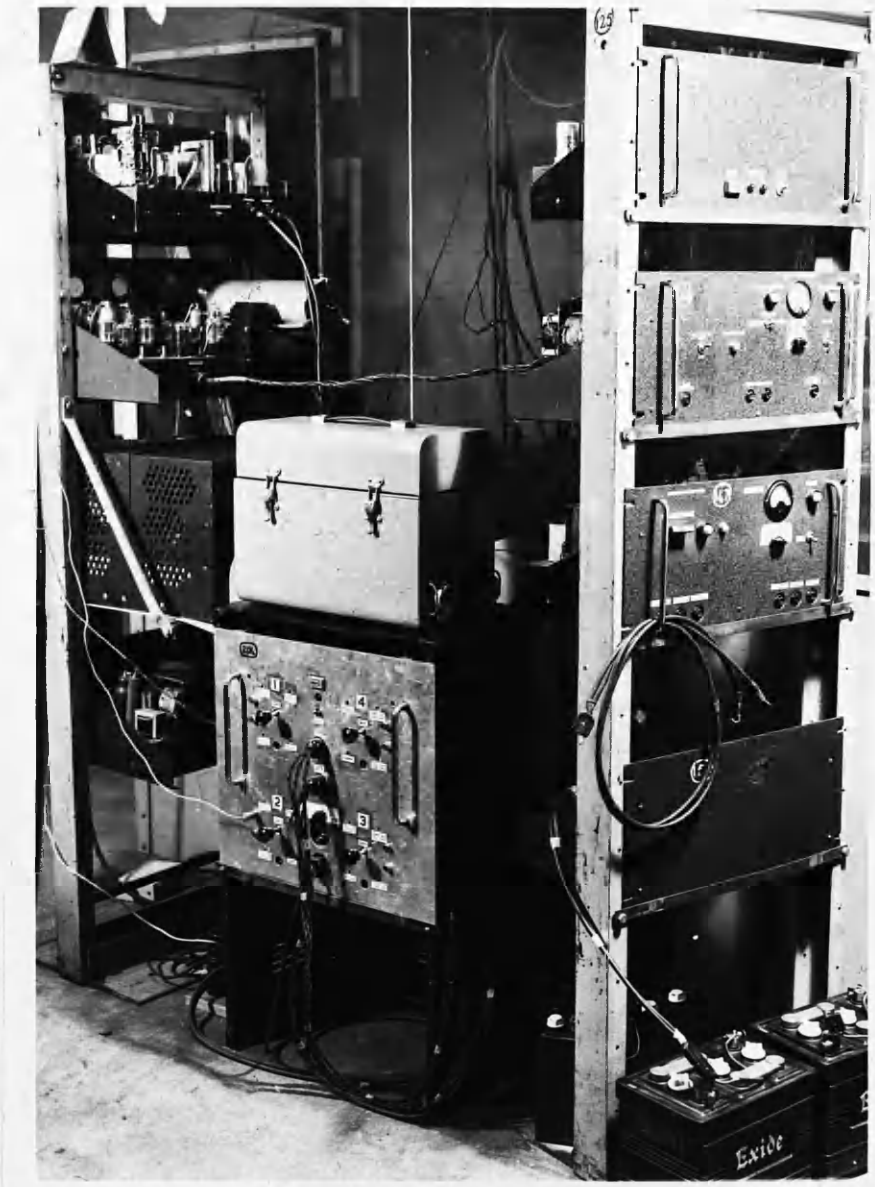



Fig. 16. The display rack outside the cage seen from the back, and the rack containing the power supply units. A pen writing recorder and amplifiers stand between the racks; this recorder was used in later experiments, but not in those described in this thesis.

audiomonitor unit while conducting the experiment within the cage. A second oscilloscope tube ('away tube') and a calibrated moving coil meter to which the output of the pulse-interval meter was applied, were therefore mounted in the rack within the cage, as shown in fig.13. The audiomonitor unit, also shown here, had an adjustable suppression level so that it was possible to select the impulses to be monitored, as with the pulse-interval meter. It derived its input from either of the pre-amplifiers or from the pulse-interval meter after the selection stage. The thermal control unit, operated by the thermistor in the paraffin pool, can be seen on the top of the rack shown in fig.13.

The power units for the amplifiers, display tubes, and the pulse-interval meter were mounted in a separate rack outside the cage. This rack is shown in fig.16. At the left of the photograph the display rack is seen from behind, and in the centre is a four channel pen writing recorder which was used in later experiments but not in those described in this thesis.

In the early stages of the investigation, the nerve obtained in the dissection was stimulated to confirm that it did not contain any motor fibres to the muscles near the joint. The stimulator used for this purpose is shown in the display rack in fig.1.

## APPARATUS FOR PRODUCING JOINT MOVEMENT.

The possible movements of the knee-joint can be analysed into a number of components as follows:-

1) Changes in the angle between the long axes of the tibia and femur such as occur in flexion and extension of the knee. These movements will be referred to as 'flexion' and 'extension'.

2) Rotation of the tibia about its own long axis as in twisting the leg by rotating the foot. A clockwise rotation of the left tibia, produced by rotating the foot outwards, will be referred to as 'outward twisting of the tibia'. Anticlockwise rotation of the left tibia, produced by rotating the foot inwards, will be referred to as 'inward twisting of the tibia'.

3) Rotations of the tibia about the long axis of the femur, as in lateral and medial movements of the distal end of the tibia when the knee is partially flexed. These movements will be referred to as 'lateral (or medial) movement of the tibia'.

4) Gliding movements of the articular surfaces over one another.

5) Movements of apposition and separation of the articular surfaces when the limb is in compression or tension.

a) Flexion and extension.

Movements of flexion and extension were produced by

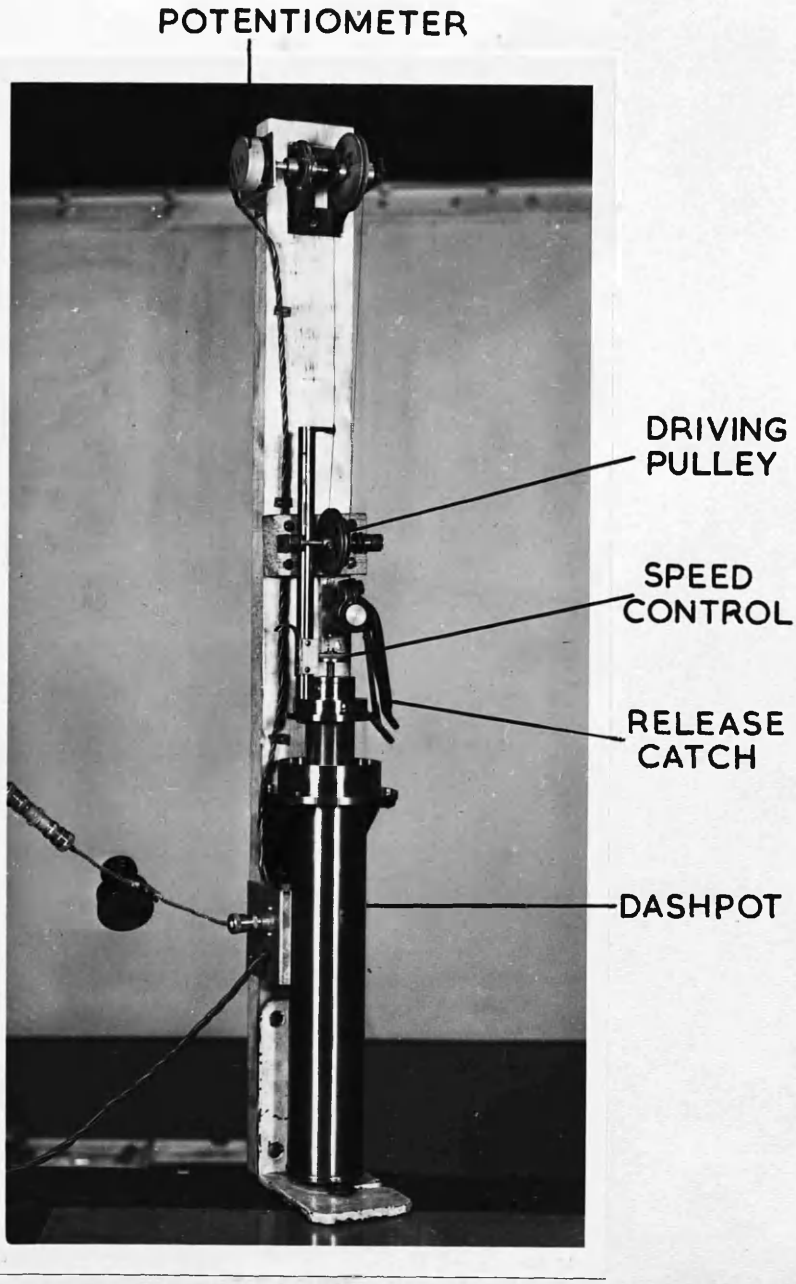



Fig. 17. The dashpot system for producing controlled movements of the joint. Fall of the dashpot at a steady controlled rate rotates the pulleys, and threads round these are arranged to produce the required movement of the joint. Movment is recorded by a vertical shift of the second beam of the oscilloscope, produced by rotation of the spindle of the potentiometer which is connected across a battery and coupled to the top pulley.

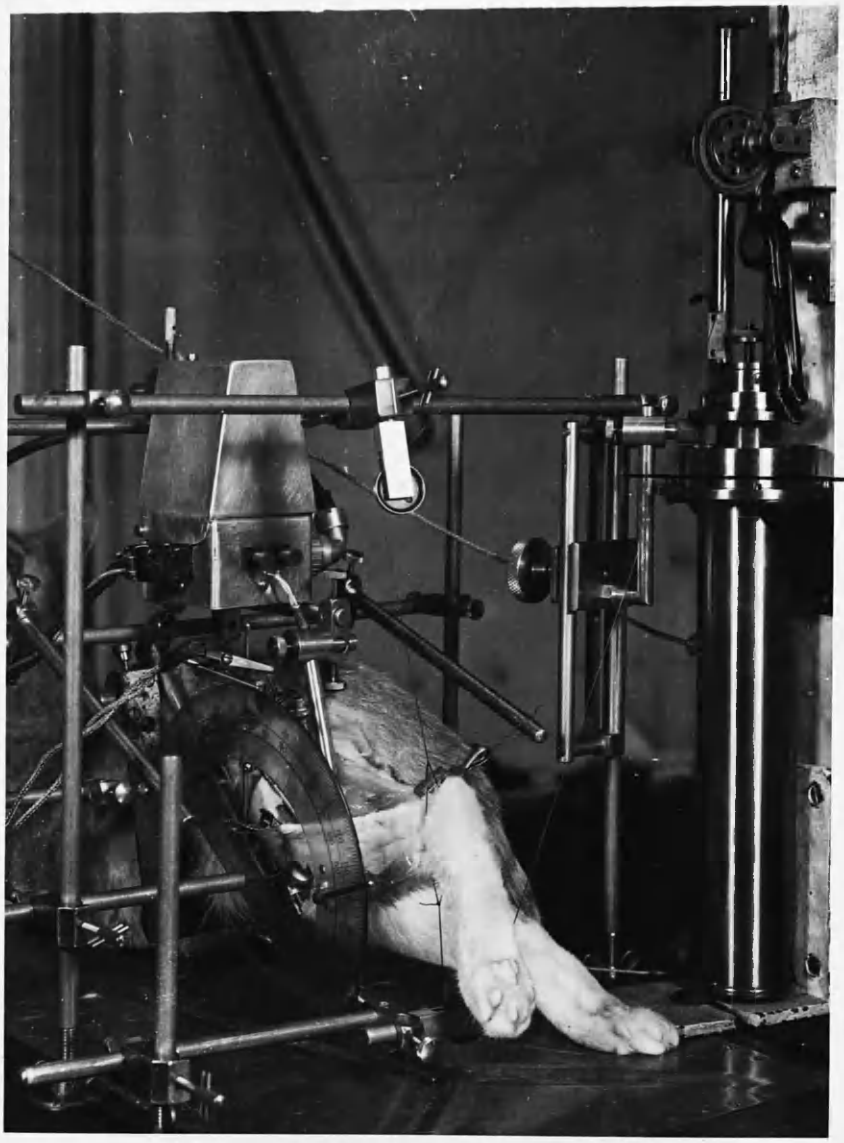



Fig. 18. The pulley system arranged so that fall of the dashpot produces flexion of the joint. The bone-pin pointer in the tibia moves over a protractor fixed as shown and the angle between tibia and femur can therefore be found at any moment. The rack clamp controls the amplitude of fall of the dashpot.

a system of threads and pulleys operated by a dashpot. This was mounted on a stand, as shown in fig. 17, so that in falling it rotated two pulleys, one at the top of the stand and the other mounted on a spindle having on it several driving pulleys of different diameters. The top pulley in turning rotated the spindle of a potentiometer which was connected across a battery. The voltage output from this system was fed through a potential divider and applied to the second beam of the oscilloscope in place of the e.c.g. signal described earlier. Movement of the dashpot was thus indicated by vertical shift of the oscilloscope beam, the amplitude of the shift being controlled by the potential divider. The rate of fall of the dashpot was controlled by the screw adjustment on top of the dashpot, the screw moving up and down a calibrated scale. The extent of the excursion of the dashpot was controlled by a rack clamp (fig.18), which determined the height of the rubber stop onto which the dashpot impinged at the end of its fall. This figure also shows the pulley and thread system by which the driving pulley was connected to the ankle of the animal, fall of the dashpot producing flexion of the limb. Although several sizes of driving pulley were available, a suitable excursion of the limb could nearly always be obtained using only the largest

Fig. 19. View of the paraffin pool over the back of the knee-joint showing the glass platform, electrodes and thermistor in position.

of these. The return movement had to be carried out by raising the dashpot onto the release catch by hand. If it was desired to study the response to extension at a steady rate, the thread system was reversed so that fall of the dashpot produced extension of the limb. The method of attaching the thread to the ankle is shown in figs 18 & 19; two loops of thread were used so that there was no 'backlash' when the direction of movement was reversed.

Changes in angle between tibia and femur were indicated by movement of the bone-pin in the tibia over a protractor, fixed in a vertical plane with its zero corresponding to the line of the femur and its centre on the axis of rotation of the knee, as shown in figs. 18 & 19. The angle between tibia and femur could be read directly in degrees of extension. The angle of insertion of the bone-pin used as a pointer could not be very accurately controlled and was probably not quite the same in each animal, though the pointer was inserted as nearly horizontal as possible. This means that the angles between the bones may have been assigned numerical values differing from the true values by a few degrees. Changes in angle were, however, accurately recorded.

If it was desired to obtain the steady values of

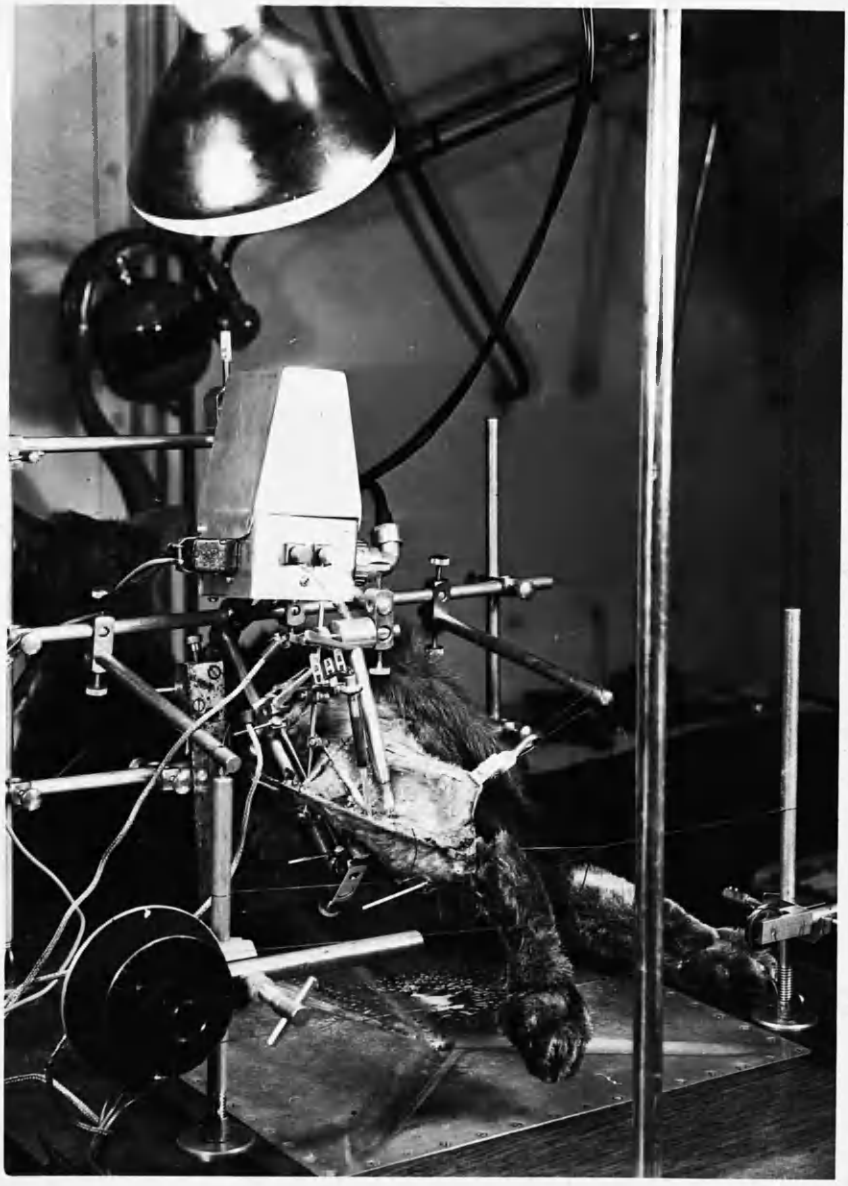


Fig. 20. The arrangement for producing twisting movements of the tibia by hand. The ankle is fixed by threads to the side supports, and clockwise rotation of the knob at the left of the picture would produce outward twisting of the tibia by means of the continuous loop of thread attached to the foot as shown.

impulse-frequency in various positions when recording the response from a slowly-adapting sensory unit, the rack clamp was slowly lowered or raised, while the dash-pot was in contact with the stop, until the pointer reached the desired position.

Because it was possible to obtain a direct reading of the limb position, and to reproduce movements accurately both in amplitude and in rate, flexion-extension movements were used in preference to other movements whenever possible. Analysis of the response to other types of movement was only carried out when a 'single-fibre' preparation was obtained which did not respond to flexion or extension, but did respond to, for example, twisting of the tibia.

b) Twisting of the tibia.

The arrangement used for producing twisting of the tibia is shown in fig.20. It was necessary first to fix the ankle and this was done with two loops of strong thread tied to the uprights as shown in the figure. Threads were then attached to the distal end of the foot and passed round two pulleys on uprights at either side of the operating table to form a continuous loop. One of the pulleys was mounted on the spindle of a potentiometer which also had a knob and calibrated dial on

it. By rotating the knob, twisting of the tibia was thus produced, either inwards or outwards, and the angle of twist was obtained by measuring the distance between the point of attachment of the thread and the axis of rotation of the tibia, and measuring the horizontal excursion of a knot on the thread. The dial readings were calibrated accordingly so that measurement of every angle of rotation produced was unnecessary. The potentiometer was connected, as in the flexion system, so that rotation of the tibia was recorded as a vertical shift of the oscilloscope beam. Since the movement was produced by hand, it was not possible to produce movement at controlled steady rates. This system for producing movement was less satisfactory than the flexion system described above.

c) Lateral movement of the tibia.

The arrangement for producing lateral (or medial) movement of the tibia was similar to that for twisting, except that the threads producing movement were attached direct to the ankle. On several occasions the dashpot-pulley system described under flexion movements was arranged to produce medial or lateral movement of the tibia. Accurate measurement of the position of the tibia, and hence accurate reproduction of the movements, was again difficult. The movement was measured directly by noting the horizontal distance travelled by a knot in the thread.

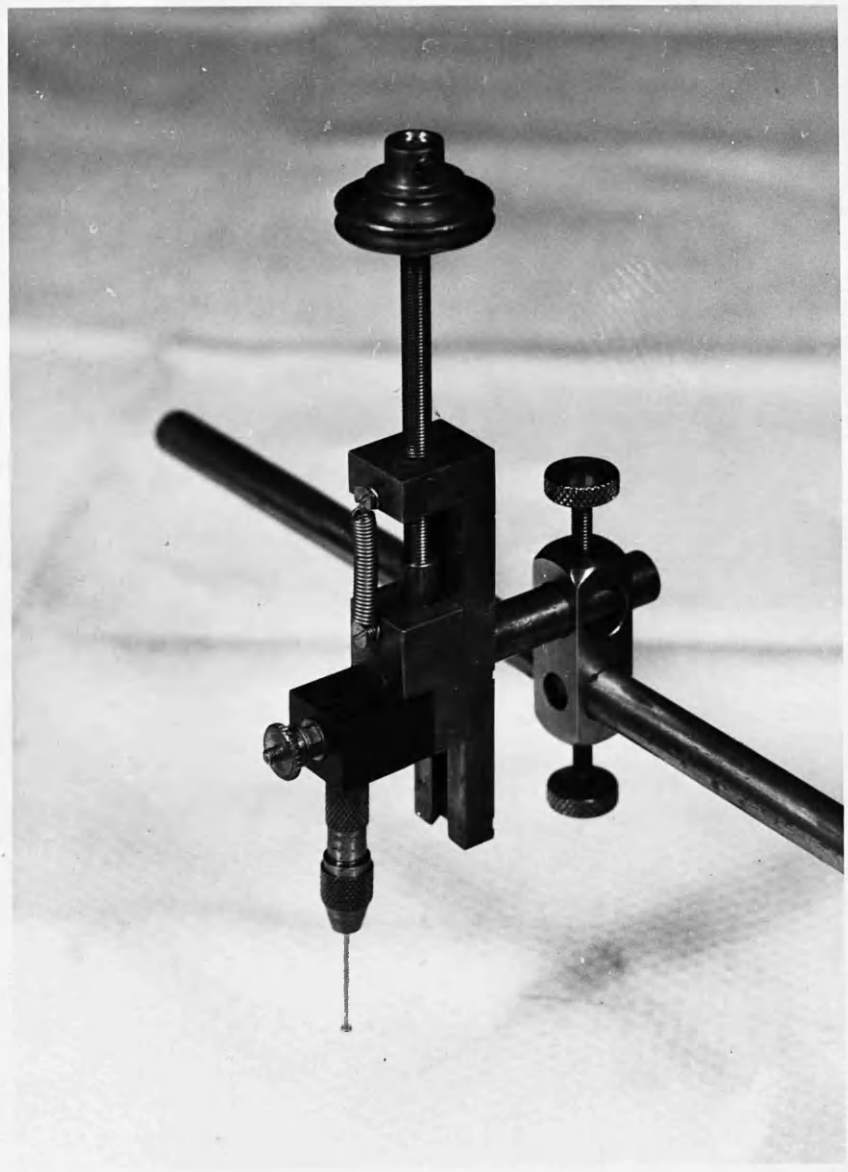


Fig. 21. Apparatus for applying controlled pressure to the joint-capsule. Rotation of the top pulleys, which are coupled to the dashpot system, produces vertical movement of the pin held in the chuck.

## APPARATUS FOR APPLYING PRESSURE TO THE JOINT-CAPSULE.

When it was discovered that direct pressure on the joint-capsule directly over a sensory unit caused it to discharge, an apparatus was devised for applying pressure at a steady rate, so that the point of application moved through a known distance, the pressure being maintained for as long as was required. The apparatus is shown in fig.21, and consisted of a modification of an electrode carrier designed by Dr.T.D.M. Roberts. Two pulleys of different sizes were fixed to the top of the spindle, a spring attached to the sliding portion so that backlash on the return movement was eliminated, and a pin was placed in the chuck, head downwards. The pulleys were driven by the dashpot system already described, so that the rate and amplitude of movement of the pin head could be controlled and adjusted. It was found that the response to pressure on the capsule with this apparatus varied from one application to another, and the arrangement did not produce much information of value. The application of controlled pressure to the capsule was therefore abandoned.

## THE SINGLE-FIBRE PREPARATION.

The discharge recorded from the whole posterior articular nerve usually consisted of the responses from many sensory units and it was not often possible to analyse the response from any one without subdividing the nerve. This was carried out beneath the surface of the paraffin in the pool over the back of the knee-joint, on a small platform of black glass. Black glass was used since it provided a contrast between platform and nerve-fibres which made small twigs of the nerve much more easily visible. The platform was mounted over the back of the joint, but towards its medial side, so that as much flexion of the joint as possible could be obtained without the soleus muscle coming up against the platform. The electrodes were mounted so that the platinum hooks were just above the surface of the platform, and could be swung out of the way while dissection of the nerve was in progress. The thermistor for controlling the temperature of the pool was fixed to the same support as the platform, and the usual relationship of the three pieces of apparatus is shown in fig.11.

The instruments employed in the subdivision of the

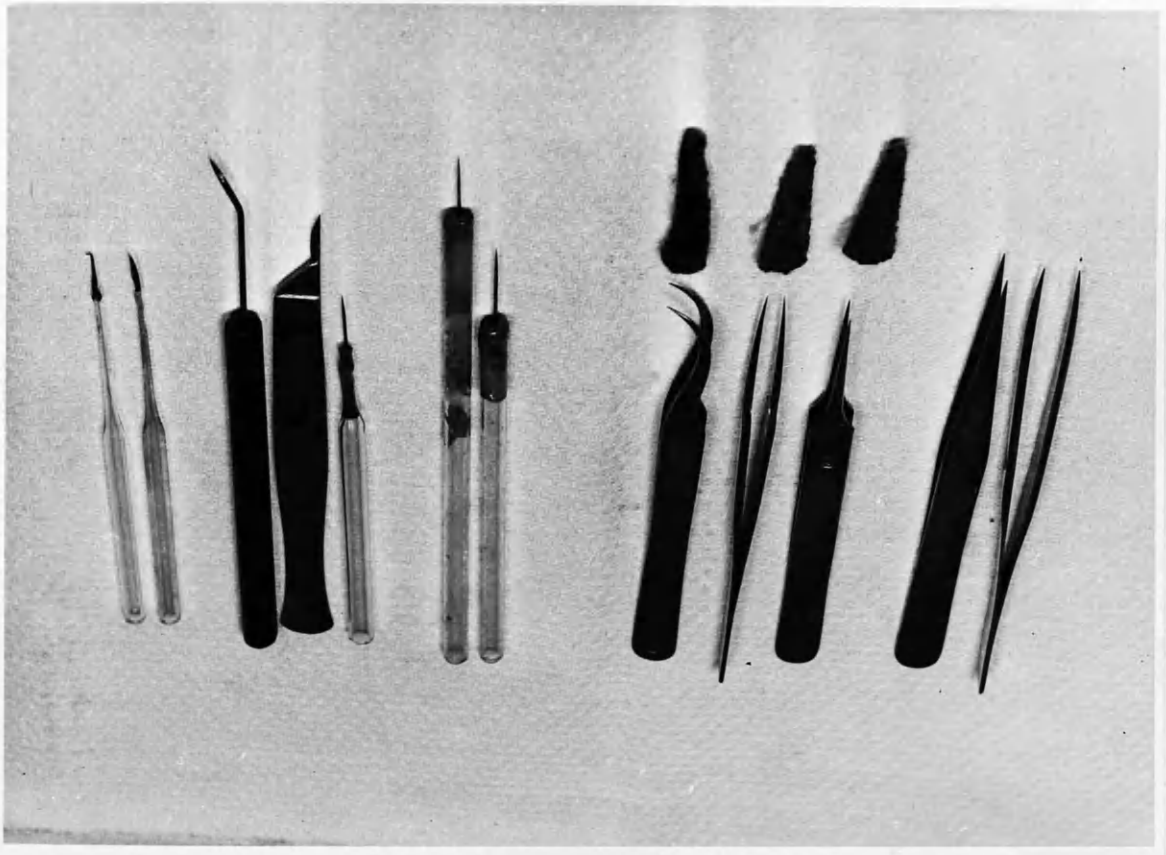


Fig. 22. Examples of the instruments used in subdivision of the nerve.

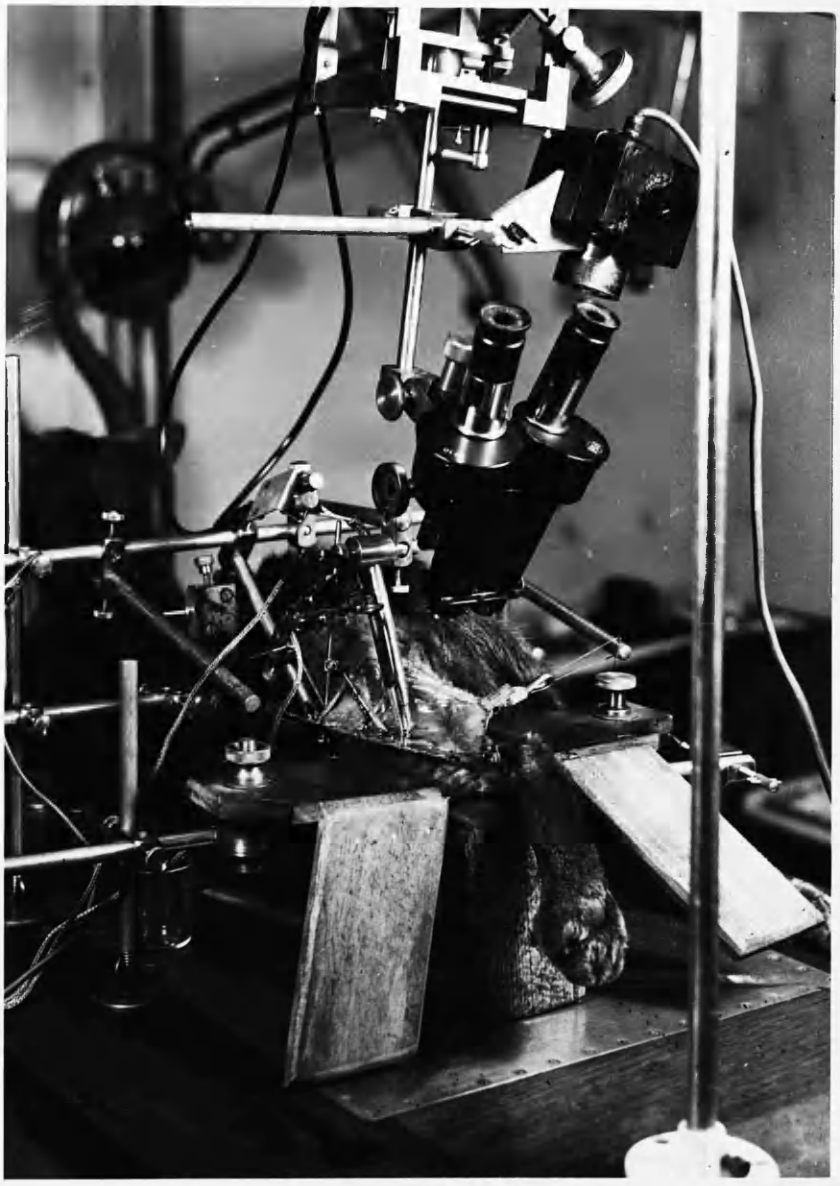


Fig. 23. Photograph showing the arrangement of apparatus during subdivision of the articular nerve. The dissecting microscope and spotlight are focussed on the nerve as it lies over the black glass platform beneath the surface of the paraffin. The arm rests for supporting the arms and hands during dissection are shown in position.

nerve were very fine straight and curved forceps, finely ground needles sealed into small glass tubes with sealing wax, and very fine scalpels. Some of the needles were ground flat at the tip producing miniature scalpels. Tungsten needles, with fine points produced by dipping the needles into sodium nitrite solution, were used on some occasions, but were found to bend too easily if they came in contact with the glass platform. Small black glass hooks of various shapes were also found useful for separating and lifting small twigs. Examples of these various instruments are shown in fig.22.

Subdivision was carried out under a binocular dissecting microscope mounted on a stand completely separate from the operating table, the stand being fitted with micro-adjusting screws by means of which small movements of the microscope in any desired direction could be produced. The glass platform was illuminated by a spotlight mounted on the microscope stand, so that wherever the microscope was moved the field remained illuminated. Fig.23 shows the microscope and spotlight in position. Also visible are the arm rests used during the dissection. It was found impossible to control the tips of the dissecting instruments properly unless the

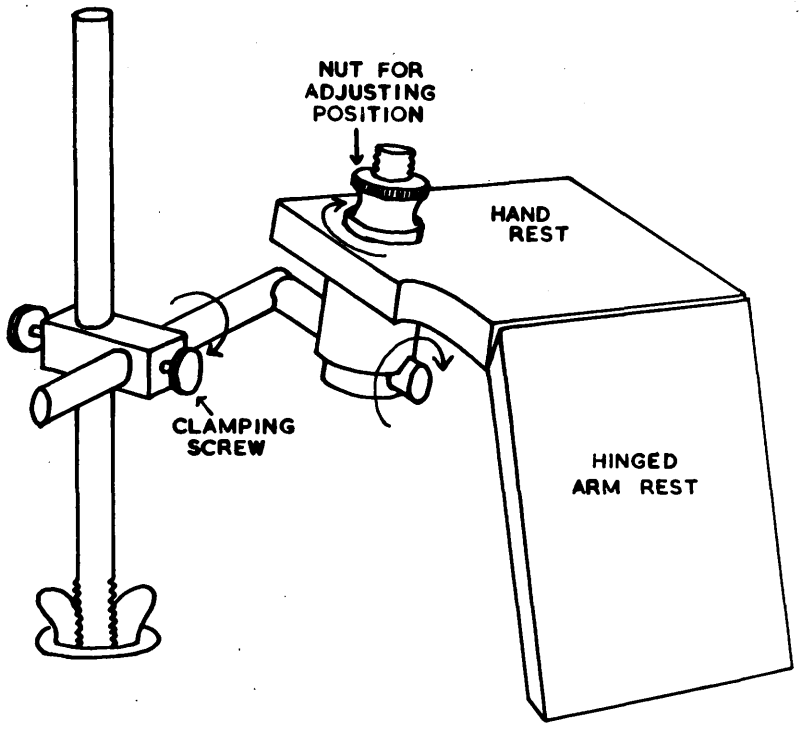



Fig. 24. Diagram showing the arm rests in detail. Adjustment of the rest into any desired position could be carried out by the adjusting nut and the clamping screw.

arm and hand were supported over the pool. The arm rests were therefore designed to make this possible. Fig.24 shows these rests in detail; they consisted of a small platform for the hand, with a sloping, hinged, support for the arm. The platform was mounted on a brass rod clamped to an upright on the operating table, so that its height could be adjusted, and the single knurled screw on the platform, and the clamping screw on the upright, enabled it to be set at any desired angle.

Before commencing the search for a 'single-fibre' preparation, the sweep speed of the oscilloscope was adjusted so as just to give the appearance of a single line on the screen. This meant that a number of action-potentials could be observed on the screen at once, even if the frequency of discharge was low. An action potential, which with a faster sweep speed would have been similar to the one shown in the top left corner of fig.25, then was visible as a single vertical line, as in the top right hand corner of the same figure.

The whole articular nerve was laid over the electrodes so that a region near the cut end was in contact with the platinum hooks. The joint was then moved in various directions to elicit a discharge in the

nerve. If no discharge occurred this usually meant that the nerve had been damaged in the earlier dissection. This was quite common in the earlier experiments, but as experience was gained in the dissection damage occurred to a lesser extent. It was found that the nerve was most easily damaged by lateral pressure applied with the dissecting instruments when separating it from surrounding tissues, especially if any kinking of the nerve was produced. Severe traction on the nerve also caused damage, but if slight traction was applied and the tissues were dissected away from the nerve so that it was not itself actually touched, it was nearly always found to be active along its whole length when put on the electrodes. If no response could be obtained on movement, the nerve was moved over the electrodes gradually until an active region was found. Since the nearer the electrodes were to the back of the joint the more restricted were the movements which could be carried out without disturbing the fibre on the electrodes, it was obviously desirable that subdivision of the nerve be carried out as far from the joint as possible. The maximum length of nerve available was about 3 cm, and often much less.

The articular nerve, obtained by the dissection

already described, was surrounded by a considerable amount of connective tissue, the apparent diameter of the nerve being about twice its true diameter, which was about 0.2 mm. This connective tissue was removed by separating it from the nerve at one point so as to form a small loop - this could be done by placing a needle on either side of the nerve between it and the connective tissue, and gently pulling each needle away from the nerve. The loop of connective tissue was then gripped by two pairs of forceps so that their tips were close together, and the forceps were then separated and gently pulled apart up and down the length of the nerve. The connective tissue between them divided and the rest was stripped off for a few mm in either direction. No lateral pressure was therefore exerted on the nerve and it was never found to be damaged after the connective tissue was removed in this way. A portion of the nerve about 1 cm long was completely cleaned of connective tissue. The whole nerve was then replaced on the electrodes and the amplitude of the action-potentials of the discharge in the nerve was almost always found to be greatly increased, though still consisting of a number of units.

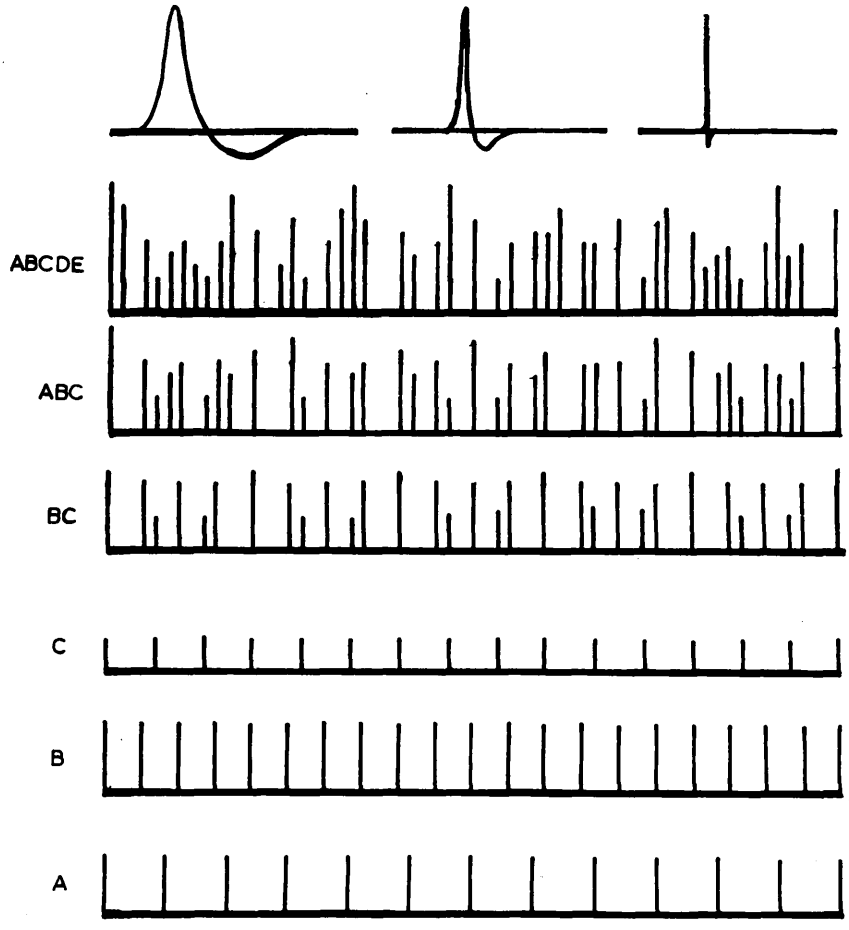



Fig. 25. Diagrams of action-potentials recorded from a nerve. In the top left hand corner is shown an action-potential as it would appear on the oscilloscope with a fast sweep frequency. The two small figures beside this show the effect of reducing the sweep speed. The other diagrams show the type of discharge to be expected when recording from a twig containing 5, 3, 2 or 1 units, each discharging with steady impulse-frequency.

Fig.25 is a diagram of the types of discharge recorded from a nerve in which a varying number of sensory units contribute to the response. ABCDE is the kind of picture seen on the oscilloscope when five units, each discharging at a different steady frequency, are involved. The picture is complex and it is very difficult to analyse the response from any one unit. ABC might be the recorded discharge when the nerve of ABCDE was subdivided. Units D and E have been removed in the process. Here it is possible to distinguish the responses of the different units, but if the frequencies of the impulses from each unit were changing, e.g. during a movement of the joint, it would again be impossible to differentiate the responses of the three units. Further subdivision might result in a twig being obtained in which only units B and C were active. The picture would then be as in BC. If a preparation were obtained in which only one unit was active, the appearance would be as in A, B or C. Such a preparation is termed a 'single-fibre' preparation, even though recording is being carried out from a nerve containing more than one nerve-fibre, there being present other fibres from sensory

units which are not active in this position of the joint. For detailed analysis a 'single-fibre' preparation is to be preferred, though a twig containing two active units is sometimes satisfactory where the impulses are recorded on photographic film. However, if the pulse-interval meter is employed, it is essential to have only the impulses from one sensory unit triggering the instrument. This can only be achieved from a 'single-fibre' preparation, or one containing a response composed of action-potentials of much greater amplitude than that of any others present. The trigger level of the pulse-interval meter could be adjusted so that only the large action-potentials triggered the instrument.

It was found that as the experiment progressed fewer and fewer fibres in the articular nerve remained active. Presumably this was due to death of some of the fibres as a result of the abnormal conditions to which the nerve was subjected. It sometimes happened, therefore, that at the commencement of recording most movements of the joint elicited massive discharges in the nerve,while after some hours similar movements resulted in activity in only a few fibres. By moving the nerve to and fro over the electrodes, and twisting it in the process so that a different portion was in contact with them, it was

sometimes possible to obtain a 'single-fibre' preparation without subdividing the nerve at all. The 'action-potential to noise' ratio in such a case was usually very large, perhaps 10 to 1, but there were certain disadvantages The range of movement over which only one unit responded was usually very limited, other units, often in large number, being excited by more extreme movements; it was very difficult to localize such a response (see later) since pressure on the capsule of the joint usually elicited a massive discharge. Because of this latter factor, such preparations were of little use where it was desired to dissect out the sensory unit from the joint-capsule, as every movement of the capsule during dissection produced a discharge which completely obscured that from the sensory unit to be isolated.

The main difficulty in subdivision lay in the removing of the nerve sheath without damage to the fibres contained in it. Whereas this proved fairly simple with a nerve like the vagus, it was extremely difficult to do this successfully on a nerve as small as the posterior articular nerve. Three methods were attempted; in the first the fibres at the cut end of the nerve were separated into two bundles each of which was gripped in fine forceps and gently separated. The sheath slid down the nerve forming a 'collar' and the fibres could then be

separated. This procedure was almost invariably found to damage all the fibres in the nerve and was therefore abandoned. The second method consisted of laying the nerve across the glass platform so that the cut end was directed towards the operator, gripping the end of the nerve with forceps and slitting the sheath by inserting the tip of a very fine scalpel, with the edge of the blade uppermost, under the sheath and sliding it along the nerve, taking care not to press down on the nerve-fibres themselves This was successful in a few cases, but the nerve was damaged on most occasions. The third method consisted of gripping the nerve fibres at the cut end with forceps, then the sheath at the cut end with another pair of forceps, and drawing the sheath down the nerve, so that it lay along the next portion of nerve, inside out. Provided the sheath slid back without forming a constricting collar, this was the method which met with most success.

When the sheath was removed, some bleeding from the nerve could always be observed if it were undamaged. If no bleeding occurred, the nerve was usually found to be damaged. On replacing the portion of the nerve, from which the sheath had been removed, on the electrodes the discharge was found to be of much smaller amplitude than it was before the sheath was removed. Sometimes no visible discharge could be elicited at all. At first this was

taken to indicate that the nerve had been damaged during removal of the sheath, but it was soon discovered that smaller twigs could be active although larger ones of which they were previously part showed no visible discharge. Once, when the sheath was pulled back again to recover the exposed nerve-fibres, a discharge with a large 'action-potential to noise' ratio, such as had been present before the sheath was removed, was found to be present once more. This only happened on one occasion. Invariably the discharge that could be elicited on the whole nerve with the sheath removed was of very much smaller amplitude, and often contained many more units, than the discharge from the whole nerve with the sheath intact.

The fibres of the nerve were separated into several bundles by teasing the cut ends apart with needles, and then separating the bundles by gripping their cut ends with forceps and gently pulling the forceps apart. It was never found satisfactory to touch the portion of nerve which would be in contact with the electrodes with the forceps or needles, so that all teasing was done at the cut ends of the fibres. Each bundle was then put on the electrodes in turn and the joint moved in various directions to elicit a discharge. The bundle was then

divided into smaller twigs.

For the reasons mentioned when describing the methods for producing and recording joint movement, the best form of 'single-fibre' preparation was one which showed a change in impulse-frequency during flexion and extension of the joint. During subdivision of the nerve, therefore, some systematic selection of this kind of unit was adopted. When a twig was placed on the electrodes, the joint was flexed and extended to elicit a discharge. If there was no response on flexion or extension the twig was usually discarded. If there was a response to these movements the twig was subdivided as before and each portion tested in the same way, the one giving the greatest discharge on flexion and extension being retained and subdivided further. When a stage was reached at which the individual units were recognisable the part of the twig containing a flexion or extension unit was retained after each step of division, until a single-fibre response of this type was obtained. Often a particular unit among others was selected as suitable and this was followed through successive stages of subdivision until it was obtained alone, or was larger and quite distinct from any others present. In many cases, though, the desired unit was lost during the division process. If at

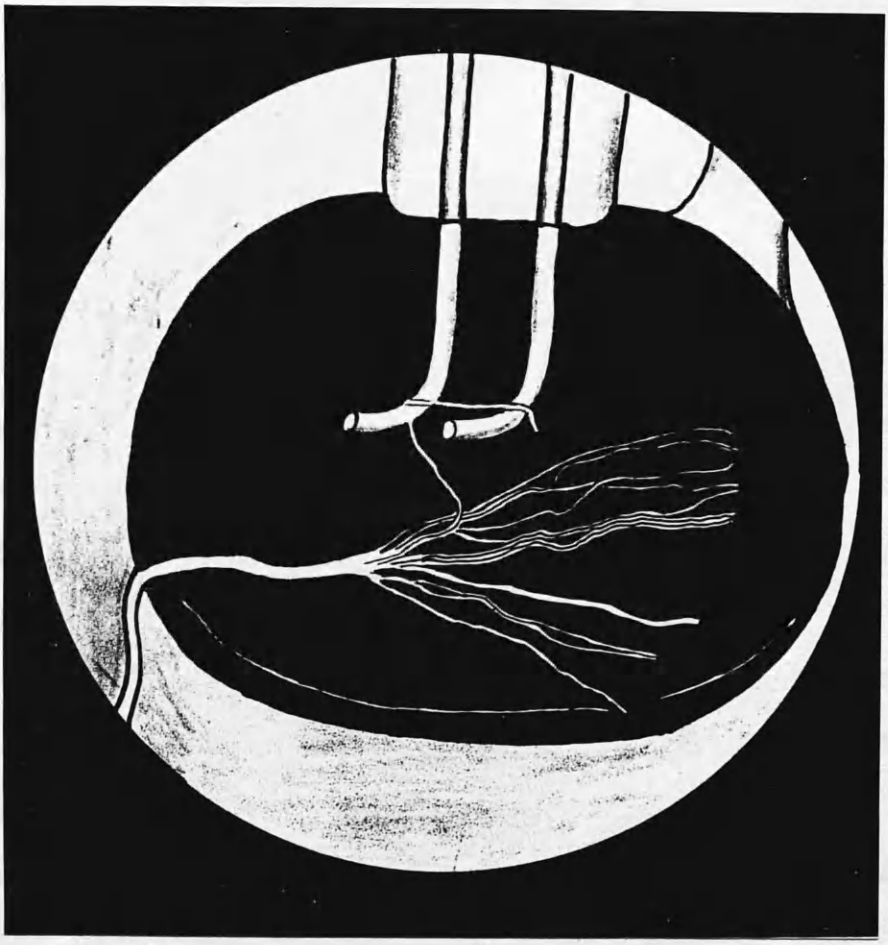


Fig. 26. Diagram of the field visible through the dissecting microscope using a low power objective, during subdivision of the nerve. The articular nerve lies on the black glass platform, the sheath has been removed from part of it, and a twig has been placed over the electrodes. A twig of this order of size relative to the whole nerve would be classed as 'large'.

any stage a good single-fibre response of another kind was obtained by chance (e.g. responding on twisting of the joint), then analysis of this response was carried out.

Fig.26 is a diagram showing the view which may be seen through the microscope during subdivision of the nerve. The articular nerve can be seen on the black glass platform and a twig has been separated from it and placed over the electrodes. Comparing the size of this twig with the size of the whole nerve on the platform, this twig would be classed as of large size, containing a considerable number of nerve-fibres. A 'small twig' as described here, would be only just visible on the same scale.

With small twigs the amount of 50-cycle interference was considerable, due to the high impedance at the electrodes, and to reduce this a cathode follower was added to the recording apparatus. It was placed as close to the electrodes as possible (see fig.20), so that the long leads from the operating table to the recording apparatus connected cathode follower and preamplifer, and the portion of leads between electrodes and cathode follower was very short. In this way 50-cycle interference was reduced to a minimum, and at the same time the 'action-potential to noise' ratio was considerably increased.

It was found that recording could be carried out close to the cut ends of the nerve-fibres without any interference due to injury potentials etc., and the end of small twigs could be wound round one of the electrodes so that the twig was not likely to be displaced during movement of the joint. It was frequently found that twigs, which were so small that the usual method of subdivision was impossible, still contained many active fibres. The central end of such a twig was then wound round one of the electrodes so that the twig lay over the leading electrode. A needle was placed beneath the twig between the electrodes and was slid along the twig in a central direction lifting the twig off the leading electrode in the process. Stroking the twig underneath in this way produced gradual division of the fibres in it and the number of active units in the twig was slowly reduced, until on some occasions a single-fibre preparation was obtained. More often, however, twigs which were so small that it was difficult to see them under the microscope were still found to contain two or three active units. It therefore seems doubtful if recordings were ever made from a true single fibre.

When fine twigs were on the electrodes it was important to prevent other fibres from touching the leading

electrode, as the discharge then contained the responses carried by these other fibres as well as from those in contact with both electrodes. This gave the impression that there were more active fibres in the twig across the electrodes than were actually present.

The 'action-potential to noise' ratio for units on small twigs was always small - rarely more than 2 or 3 to 1 - and all units present were of about the same amplitude. With larger twigs, on the other hand, the amplitudes of various units differed considerably (presumably due to the relation between the particular fibre in the twig and the electrodes) and the 'action-potential to noise' ratio was often large. In all cases this ratio was found to increase for some time after the twig was first placed over the electrodes.

It will be seen that there were disadvantages in recording the response of one unit from both very large twigs and very small twigs. These may be summarized as follows:-

Disadvantages of large twigs:

a) The range of movement was restricted since greater movement initiated discharges in other fibres.

b) Pressure applied to the capsule in an attempt to localise the unit produced massive discharges of other units not activated by the particular movement of the joint.

Disadvantages of very small twigs:

a) A small 'action-potential to noise' ratio was common, making triggering of the pulse-interval meter erratic, or identification of action-potentials on photographic records difficult.

b) Action-potentials of different units were of about the same size. Selection of one unit from among others by adjusting the trigger level of the pulse-interval meter was therefore impossible i.e. only a single-fibre response was suitable for analysis.

The aim in each experiment was, therefore, to obtain a unit responding on flexion or extension of the joint on a twig small enough for there to be no other large units activated in the desired range of movement, but not so small that the action-potentials of the unit could not be selected by the pulse-interval meter, or distinguished on photographic records, from the amplifier 'noise' or the responses of other units present. In the experiments where histological examination of the sensory unit responsible for the discharge was carried out, the twig had to be smaller than in the other cases so that localization of the unit in the capsule was possible.

Using the method described of recording from nerve-twigs beneath liquid paraffin at a controlled temperature,

a single-fibre preparation usually remained active for a considerable time. Recording from larger twigs was often continued for several hours while analysis of the response was carried out, and even very fine twigs remained active for periods of half an hour or more.

The process of subdividing the nerve until a suitable preparation was obtained often took many hours. Sometimes the whole nerve was subdivided until all portions of it had been examined without a suitable preparation being obtained. The nerve was then moved over the electrodes until an unused part was obtained and the whole process of subdivision was repeated with this. The procedure was found to be very tiring and the limiting factor was often shakiness of the hands of the operator which made further dissection of fine twigs impossible. In most experiments, however, at least one suitable preparation was obtained, although recording from the whole nerve was used on a number of occasions where subdivision was unsuccessful.

## LOCALIZATION OF SENSORY UNITS.

In many experiments attempts were made to localize the sensory unit responsible for the recorded discharge. A single-fibre preparation was obtained and, by moving the joint, it was determined whether it was slowly-adapting or rapidly adapting. Then the sensory unit responsible was localized by the following procedure.

If the response was slowly-adapting the knee was set in a position in which the sensory unit was discharging steadily, and the capsule was then explored with a probe until a region was found in which light pressure produced an increase in the frequency of the discharge already visible on the oscilloscope. It was not regarded as satisfactory just to produce a discharge by pressure where no discharge had been present before. A discharge produced in this way might come from a unit whose afferent fibre was contained in the twig over the electrodes but which was not stimulated by the movement producing the particular single-fibre discharge under investigation. It was usually possible to find a small area where the frequency change on pressure was a maximum, and the sensory unit was considered to lie within this area. On a few occasions no area of capsule could be found where pressure would increase the frequency of the discharge.

In these cases the sensory unit was assumed to lie in an area of the capsule inaccessible to the probe.

If the response was rapidly-adapting, localization was less simple since pressure over a rather wider area produced a response, and it was more difficult to be certain that the unit stimulated by pressure was, in fact, the one which responded on movement of the joint. However, localization of a unit of this type was considered adequate if (a) a discharge was produced on application and on release of pressure, there being no maintained discharge while constant pressure was applied, (b) the action-potentials of the discharge on pressure were of the same amplitude, as seen on the oscilloscope, as were those produced by movement, and (c) the output of the monitoring loudspeaker was of similar pitch and intensity for an action-potential produced by pressure as for one produced by movement of the joint.

## HISTOLOGICAL TECHNIQUE.

The staining method employed to demonstrate the types of receptor present in the tissues of the knee-joint was the modified gold chloride technique of Gairns (1930). Portions of the capsule from different areas of a number of knee-joints were stained and examined by this method, which involved the following stages:-

1. The piece of joint-capsule, together with several small pieces of the soleus muscle, were placed in a solution of 1 part formic acid (specific gravity 1.22) and 3 parts freshly filtered lemon juice, and the solution was left in the dark for 10 min. The muscle was included to prevent over-impregnation of the small piece of capsule, and to provide a control of the efficacy of staining of nerve elements in the capsule.
2. The solution was decanted and the tissues placed between the folds of a clean towel and pressed gently to absorb excess fluid.
3. The tissues were transferred to 1% gold chloride and returned to the dark for a further 10 min. At the end of this period excess fluid was removed as in step 2.

4. The tissues were transferred to 25% formic acid and kept in absolute darkness for 24 hr.
5. Excess fluid was again removed as in step 2, and the tissues were placed in pure glycerine and allowed to stand in full daylight for several days.

The amount of the gold chloride and formic acid solutions used was small - just sufficient to completely cover the tissues. This was important as the use of too much gold chloride, for example, resulted in such dense impregnation of the connective tissue in the specimen that it was impossible to identify the nerve elements present.

Microscopical examination of the stained tissue was then carried out. The muscle was first examined by placing a small portion on a slide in glycerine and covering with a cover glass, and the degree of staining of the motor end-plates on the muscle fibres was noted. This gave an indication of the probable intensity of staining of the receptors in the specimen of capsule, and so facilitated their location. The piece of capsule was then examined by placing it in glycerine under a cover glass; the centre of the specimen was always too dense at this stage for nerve elements to be visible, so search was made round the edge for a portion stained deep purplish-red in which a nerve-trunk was visible. Part of the piece of capsule including this was then separated from the rest, by cutting

rather than teasing, and transferred to another slide. Pressure on the cover glass over this portion was then usually sufficient to make identification of the main branches of the nerve-trunk possible. Further subdivision of this piece of capsule made it possible to identify individual receptors. If these were well stained, an attempt was made to separate individual axons, with the sensory unit they supplied, from the rest of the tissue. A binocular dissecting microscope was found most suitable for this purpose, and in a number of cases it proved possible to isolate individual sensory units and mount them together with their supplying nerve-fibres.

All the areas of the piece of capsule which were well impregnated were examined in a similar fashion.

## THE ISOLATION OF DISCHARGING SENSORY UNITS.

Since more than one type of sensory unit was found on histological examination of the tissues of the joint, it was necessary to correlate structure with type of response. An attempt was therefore made to isolate a single sensory unit from the joint-capsule, while recording its discharge from a 'single-fibre' preparation from the posterior articular nerve. It soon became obvious, however, that the sensory units in the capsule were so numerous that isolation of a single unit in the functioning state would not be possible. It was therefore decided (a) to obtain a single-fibre preparation; (b) to classify the type of response, and if it was slowly-adapting to take readings of the adapted frequency in a number of positions; (c) to localise the sensory unit as accurately as possible by the method previously described; (d) and then, while still recording the response of the sensory unit from the articular nerve, to separate from the rest of the joint-capsule a small piece containing the sensory unit.

Step (d) was carried out as described below, while listening with the loudspeaker to the discharge from the sensory unit. An incision was first made in the capsule on the side of the unit furthest from the centre of the back of the capsule i.e. furthest from the point of entry

of the articular nerve into the capsule. Then incisions were made craniad and caudad to the point where the sensory unit was thought to lie, and the process of separation continued until the discharge ceased on severing the afferent fibre from the unit. The piece of tissue thus partially separated was then removed completely, together with just sufficient of the rest of the capsule to make it reasonably certain that the localized unit was within the portion removed. The extent of the isolation of the unit obtained depended on the amount of dissection which was completed before the supplying nerve was severed, and the more complete the isolation the smaller was the piece of tissue removed.

There were two main difficulties encountered during this process of dissection; (1) if a large blood vessel in the capsule were accidentally severed, the resultant bleeding could quite easily obscure the whole preparation before the flow of blood could be stopped, and it was almost impossible to complete the dissection thereafter; (2) after a few small cuts had been made in the capsule, the strains in the capsular tissue were altered, the position of the sensory unit sometimes seemed to shift slightly, and other units whose afferent fibres were

contained in the twig on the recording electrodes, but which had not previously been active, then commenced discharging. The first of these difficulties could only be overcome by experience, since with time the positions of the main vessels became familiar, and if it was necessary to cut any of them preparations could be made to clamp the cut ends at once. Where the sensory unit was found to lie directly behind the popliteal vessels over the centre of the back of the joint, these were dissected free from the underlying capsule and cut between double ligatures. Dissection had then to be completed with as little delay as possible, since the blood supply to the receptors in the capsule was markedly reduced. The second difficulty could be partially overcome by using a 'single-fibre' discharge from as small a nerve-twig as possible, so that other sensory units were not excited during dissection, and by carefully relocalising the required unit after each cut was made in the capsule. In spite of this, there were a number of occasions on which it was not absolutely certain that the unit whose discharge had been recorded was contained within the portion of capsule removed after dissection.

The piece of capsule obtained by this method was then stained as described in the last section and examined microscopically. In the histological examination

certain factors had to be considered in addition to those previously described. In the experiments where a discharge had been localized to the piece of capsule removed, it was necessary to find all the receptors present, and not just those which were well impregnated.

The probable degree of staining of receptors having been assessed by examining the endplates in the control piece of muscle, the piece of capsule was placed in glycerine on a slide. Often the piece was small enough to be examined entire; larger specimens required to be divided and each portion examined in turn. Gentle pressure on the cover glass was usually sufficient to make identification of any nerve elements possible. Areas containing nerve elements were then separated from the rest and dissected down with needles until the receptors could be seen. Every portion of the specimen was examined in detail, all portions containing nerve elements of any kind were mounted in glycerine, and the residue of capsular tissue was collected and preserved for subsequent re-examination.

The specimens of capsule were usually small enough for the staining to be fairly uniform throughout. If nerve elements were present there was never the slightest difficulty in identifying them, even though the receptors

were poorly impregnated. On several occasions nerve-fibres within the control piece of muscle were well stained whereas the motor end-plates were hardly stained at all; in these cases it was difficult to identify the receptors in the specimen of capsule, although nerve-fibres were clearly visible. If the motor end-plates in the muscle were well stained, the capsular receptors were easily identified, although often not as densely stained as the motor end-plates. The density of the connective tissue in which the capsular receptors were embedded tended to reduce the degree of penetration of the stain; this probably accounts for the variations which were encountered in the degree of impregnation of different receptors. It is possible that when the portion of capsule removed was larger than usual a few receptors were not stained and were therefore missed altogether in the examination. It is almost certain, however, that in the other cases no receptors failed completely to take up the stain, and, since each piece of tissue was examined repeatedly, it is unlikely that any receptors escaped observation. It may, therefore, be assumed that, with the exception of the particular cases in which it is stated to the contrary, ALL the sensory

units within the specimen of capsule removed were found.

If the piece of capsule contained more than one sensory unit, then they were counted and classified.

# PART 2.

## THE PHYSIOLOGICAL RESPONSES OF THE SENSORY UNITS.

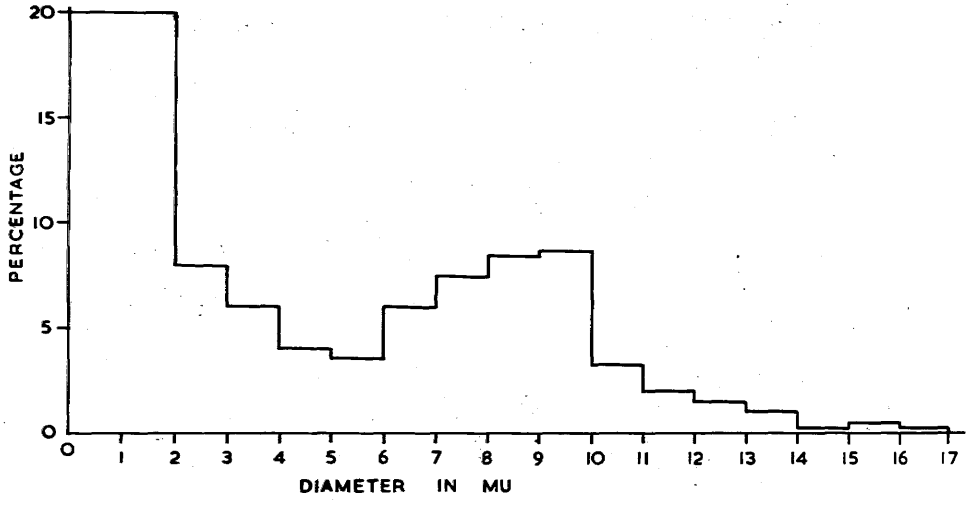



Fig. 27. Fibre-size histogram (Gardner, 1944) of the posterior articular nerve to the knee-joint of the cat, showing the numbers of fibres of different diameters as a percentage of the total number of fibres in the whole posterior articular nerve.

## REVIEW OF LITERATURE.

Almost all the information available about articular nerves to the knee-joint was obtained by Gardner, who studied their distribution, measured the sizes and conduction velocities of the fibres of which they are composed, and recorded potentials in some of these fibres as a result of stimulation of the joint-capsule (Gardner 1944; 1948b). The results of these investigations, applicable to the posterior articular nerve to the knee-joint of the cat, may be summarised as follows:

A. The posterior articular nerve has purely articular components, and gives no branches before it enters the joint-capsule. Here it divides into six or seven small branches, the axons of which accompany blood vessels in the capsule and femoral and tibial epiphyses or end within the joint-capsule in free or organised nerve-endings.

B. The nerve contains an average of 171 myelinated and 115 non-myelinated fibres; the percentage of fibres of the various diameters is shown in fig.27 i.e. there is a large non-myelinated group, less than 2 μ in diameter, a second group between 2 and 10 μ in diameter and a few fibres of larger diameter, up to 16 or 17 μ.

C. Most, if not all, of the myelinated fibres are A fibres, afferent in nature. Stimulation of articular nerves whose connections to the joint were intact never produced contractions in any of the muscles surrounding the joint, as would have been the case had the nerve contained any myelinated efferent fibres.

D. Measurements of conduction velocities suggested that the large fibres (about 16u) conducted at about 90 metres per sec, the smallest myelinated fibres (about 2u) at about 10 metres per sec and the main bulk of the myelinated fibres at about 40 to 60 metres per sec. Direct comparisons could, however, only be made between the largest fibres and the fastest rates, and the smallest fibres and the slowest rates.

E. While recording from the articular nerve, when severed from the tibial nerve but with its connections to the capsule intact, spontaneous potentials were observed, the frequency of these potentials being increased by pressing lightly on the posterior capsule with a glass rod. Incidental observations suggested that these responses were slowly-adapting but they were not studied in detail.

The results of a detailed analysis of the discharges carried by the posterior articular nerve during various

movements of the joint will now be given. The apparatus and techniques employed in this have been described in Part 1, sections 1-10.

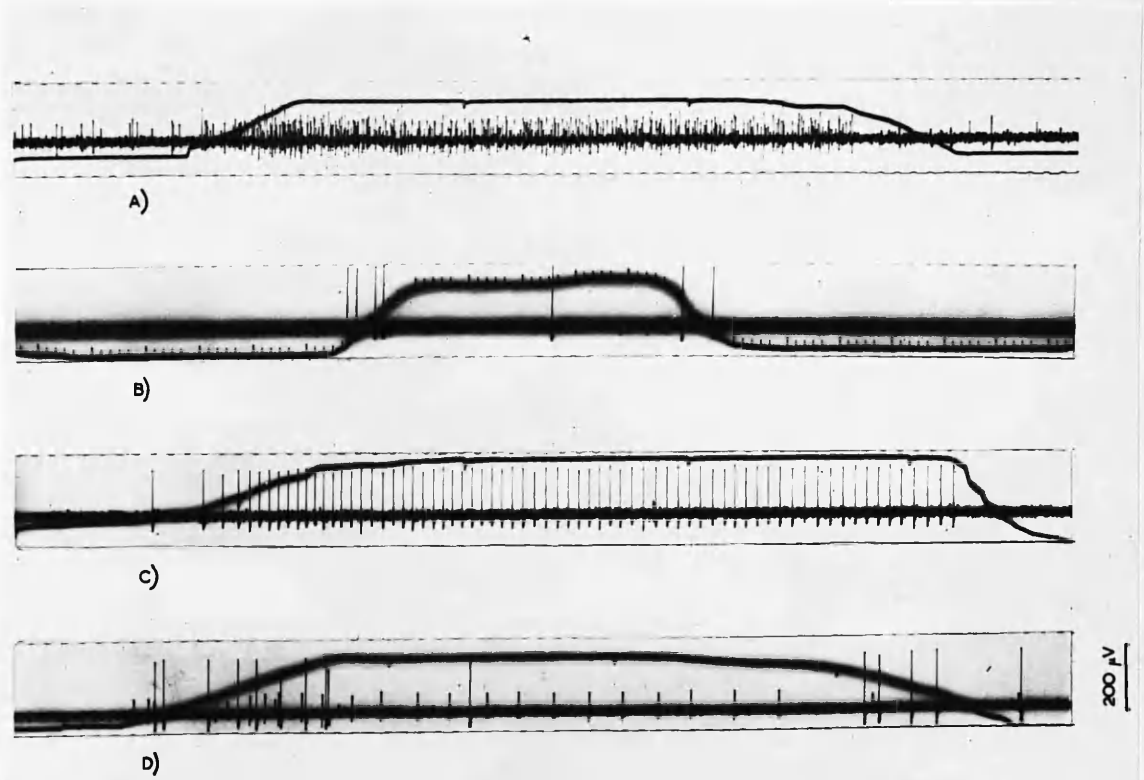



Fig. 28. Oscillograph records of discharges in the posterior articular nerve to the knee-joint of the cat. The thinner line is used to signal the movement and to carry time-markings.

A) The discharge recorded from the whole articular nerve during a movement of the knee-joint (medial movement of the tibia: prep. 58).

B) A rapidly-adapting response in which impulses occur only during movement (medial movement of the tibia: prep. 25).

C) A slowly-adapting response, the discharge being maintained in the new position (medial movement of the tibia: prep. 57).

D) The responses of two units in the same nerve-twig. The larger spikes show rapid adaptation; the smaller spikes continue until the start of the return movement. Note the relative sizes of the two types of impulse. (Extension of the knee-joint: prep. 55.)

# RESULTS.

## The response to movement of the joint.

Satisfactory preparations for analysis were obtained from 39 cats. In the observed discharges it was possible to recognise and classify the responses of 185 different units. In many cases 'single-fibre' discharges were obtained and the responses of 54 of these were analysed in some detail.

A change in the discharge could be produced by moving the joint, and almost all directions of movement were found to stimulate one or more sensory units. The possible movements of the joint have been classified in Part 1, section 7, and the terminology described there will be employed in the description of the results.

Records of typical responses obtained on recording from the posterior articular nerve are shown in fig.28. In (a) is shown the discharge from an intact articular nerve changing during a movement of the knee-joint. Subdivision of the nerve shows that the individual units can be classified into two main types: those in which impulses occur only during movement, giving similar responses to movement in opposite directions (fig.28b); and those in which movement of the joint in a particular direction produces an increase or decrease in impulse-

frequency according to the direction of movement (fig.28c). In the first type there is no discharge so long as the joint is stationary; many different types of movement may elicit a 'burst' of impulses in the same unit; the impulses soon die away and it is not possible to produce a sustained discharge. Responses of this type will be referred to as derived from 'rapidly-adapting' sensory units. In the second type sustained discharges are common; movement of the knee-joint produces a change in impulse-frequency rather than a 'burst' of impulses; different directions of movement have different effects on the impulse-frequency; when the knee-joint comes to rest at the end of a movement the impulse-frequency undergoes a process of adaptation lasting several seconds. Responses of this type will be referred to as derived from 'slowly-adapting' sensory units. It was found that the action-potentials from the rapidly-adapting sensory units were about $2\frac{1}{2}$ times as large as those from the slowly-adapting units and this difference could not be attributed merely to differences in the conditions at the electrodes. An example is shown in Fig.28d, where one unit of each type contributes to the response.

Sensory units of either type can be made to discharge individually by direct pressure with a probe applied to

| Type of movement (see text) | No. of units |
|---|---|
| Outward twisting of the tibia only | 43 |
| Either outward twisting of the tibia or extension | 7 |
| Either outward twisting of the tibia or flexion | 16 |
| Either outward twisting of the tibia or flexion; also discharged in time with the pulse-beat | 3 |
| Either outward twisting of the tibia or medial movement of the tibia | 1 |
| Either flexion or medial movement of the tibia | 4 |
| Flexion; also discharged in time with the pulse-beat | 1 |
| Flexion | 22 |
| Extension | 31 |
| Inward twisting of the tibia | 4 |
| Medial movement of the tibia | 4 |
| Lateral movement of the tibia | 2 |
| Other movements | 3 |
| Discharging continually, uninfluenced by movement | 6 |
| Discharging in time with the pulse-beat (movement not investigated) | 4 |
| Total | 151 |

Direct pressure on the capsule produced an increase in impulse-frequency in every one of the above cases in which it was tried. A 'slowly-adapting' response to pressure was obtained in a further 22 cases in which the effect of movement was not investigated.

As the experimental procedure imposed some systematic selection, this group of units should not be taken as necessarily a representative sample of the sensory units in the capsule of the knee-joint.

Fig. 29. Classification of 173 occasions on which a recognisable single unit was encountered with a 'slowly-adapting' response, to show the procedures found to produce an increase in impulse-frequency. Each unit appears in only one category in the table.

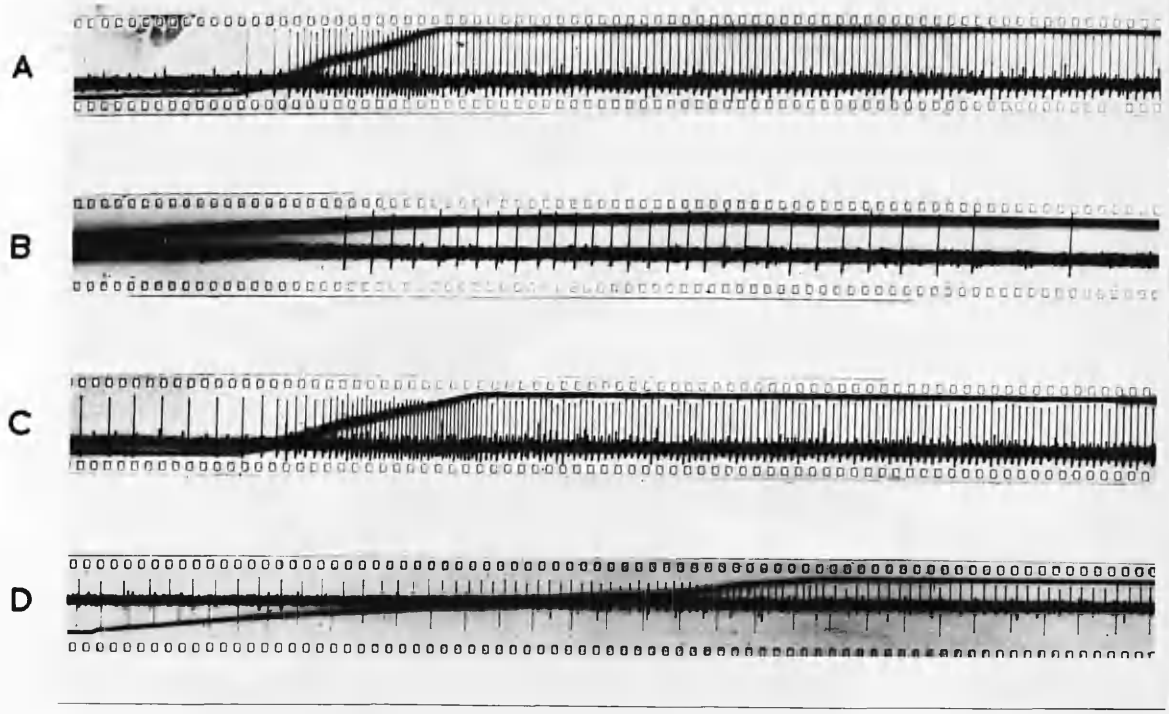



Fig. 30. Oscillograph records of discharges in twigs of the articular nerve. The thinner line is used to signal the movement.

A) The response of a slowly-adapting sensory unit to outward twisting of the tibia through 21° at a rate of 30°/sec. The discharge is maintained in the new position (Prep. 60.)

B) The response of a slowly-adapting sensory unit to outward twisting of the tibia through 25° at 8°/sec. The first impulse appeared 2 sec after the beginning of the movement (not shown) and the discharge ceases after slowing to a frequency of about 10 impulses per sec. (Prep. 14.)

C) The response of a slowly-adapting sensory unit to outward twisting of the tibia through 21° at 30°/sec, starting from a position in which there was already a steady discharge. (Prep. 60; same unit as A.)

D) The responses of two units in the same nerve-twig, during flexion of the knee-joint through 36° at 30°/sec. The spikes from the two units are recorded, by chance, with opposite polarity. Both units are slowly-adapting, and during the movement one unit shows an increase, while the other shows a decrease, in impulse-frequency. (Prep. 52: see also fig. 34.)

the appropriate area of the joint-capsule. This will be described in detail later. Of the 185 units examined only 12 were of the rapidly-adapting type; the other 173 were all slowly-adapting in type.

As each nerve-twig in turn was placed on the electrodes, various movements were tried in order to elicit a discharge or to modify a 'spontaneous' discharge, and the movement or movements producing an increase in impulse-frequency were noted for each recognisable unit. Fig.29 is a table showing the number of slowly-adapting units responding to each of the various movements attempted. Of the units in which the response to movement was investigated the largest number showed an increased discharge on 'outward twisting of the tibia'. Many of these also responded to other types of movement as indicated. No unit appears in more than one category in the table.

In Fig.30A is shown the response of a slowly-adapting unit not discharging initially but discharging with increasing frequency during movement and continuing to discharge in the new position. In Fig.30B a response is shown in which the impulse-frequency in the new position eventually decays to zero. In many cases a unit was found to be discharging steadily when the nerve-twig was

first placed on the electrodes. The corresponding 'single-fibre' response to a movement is then as shown in Fig.30C. If the joint is now moved in the opposite direction the impulse-frequency decreases, and positions can often be found on one side of which the unit does not discharge either at rest or during movement. This implies that there is a 'critical' position for the response. This will be referred to later.

The same movement may produce an increase in impulse-frequency from one sensory unit and at the same time a decrease in the impulse-frequency from another. Such a response is shown in Fig.30D, where the discharges from two sensory units were picked up from the same nerve-twig. The action-potentials of the two units appear, by chance, with opposite polarity, and show frequency changes in opposite senses during the movement.

The impulse-frequency was plotted against time for each of the records obtained. As the records were often rather long, not every interval between impulses is represented in the graphs. At appropriate points in time (usually $\frac{1}{4}$ sec intervals, but smaller intervals if the frequency was changing rapidly) several measurements were made of the intervals between successive impulses, and the average of these was used to derive the frequency

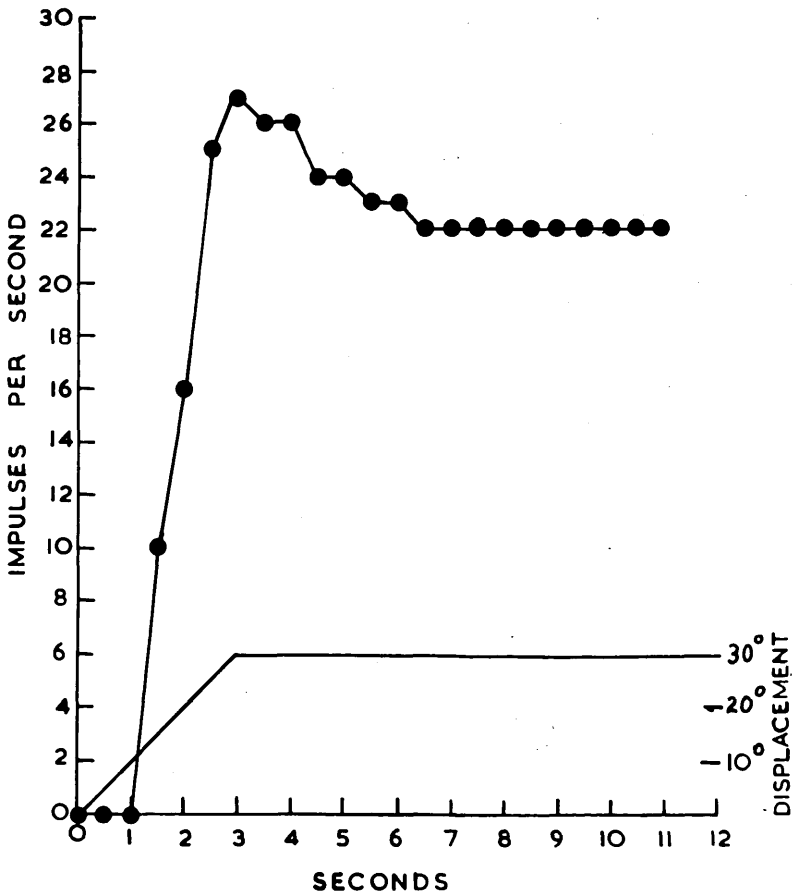



Fig. 31. Graph of the response of a single, slowly-adapting sensory unit to a movement of 30° of outward twisting of the tibia at 10°/sec. There is no initial discharge, the impulse-frequency increases during the movement to a peak value and thereafter decays slowly until it reaches a steady value of 22 impulses per sec. (Prep. 29.)

at this point. This frequency was usually plotted to the nearest whole number of impulses per sec. The scatter of the measurements rarely corresponded to a frequency difference of more than one impulse per sec, so that there were no marked fluctuations in frequency which this method of measurement might have concealed due to the averaging of the time occupied by several neighbouring intervals. A record of the type shown in part in fig.30A gives rise to a graph of the form shown in fig.31, which shows the response of a sensory unit to 30° of outward twisting of the tibia. During the movement there is a marked rise in impulse-frequency followed by a slow decay in impulse-frequency until a steady value is attained. The time taken for this adaptation to a steady value varies from one sensory unit to another, and depends on the velocity of movement and on the final value of the impulse-frequency, but in general the frequency approaches within 1 impulse per sec of its ultimate steady value within 10 secs. Many units show complete adaptation within 7 secs, but a few show some further slight decay in frequency for periods of up to 1 min. The much greater impulse-frequency attained during the movement than that ultimately reached after the movement ceases, will be referred to as the 'exaggeration' of the response, the

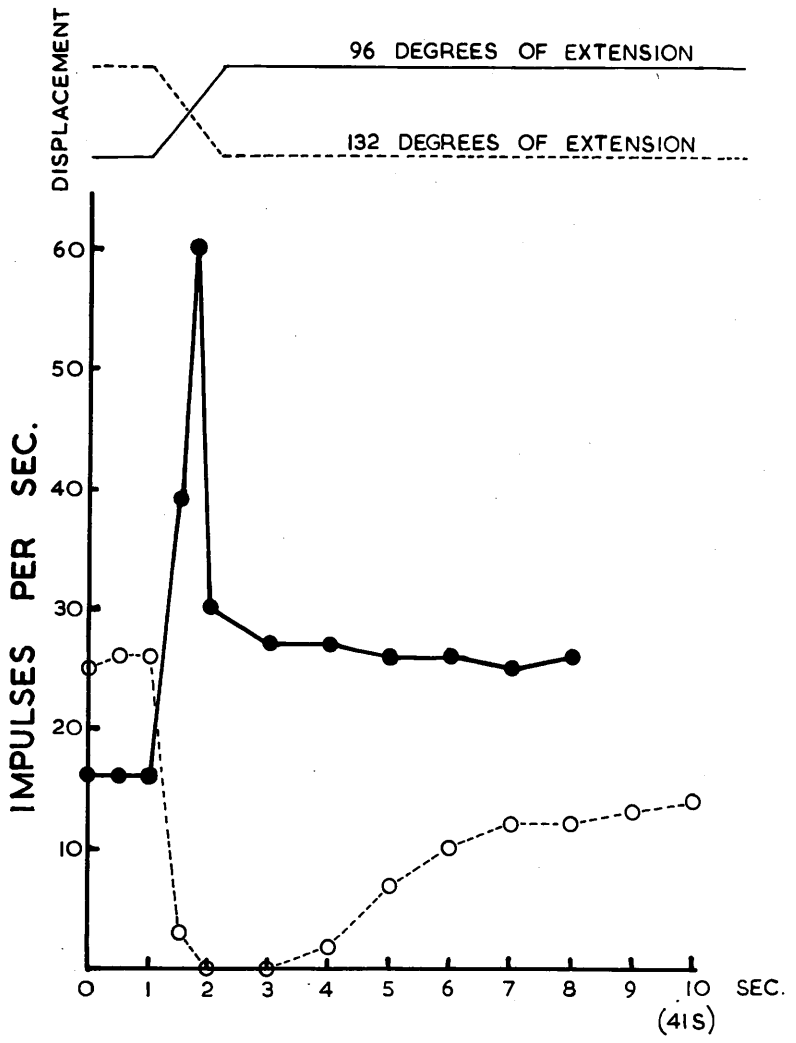



Fig. 33. Graph of the response of a slowly-adapting sensory unit to two movements in opposite directions between the same two positions. The corresponding displacements are shown above. (Prep. 52.)

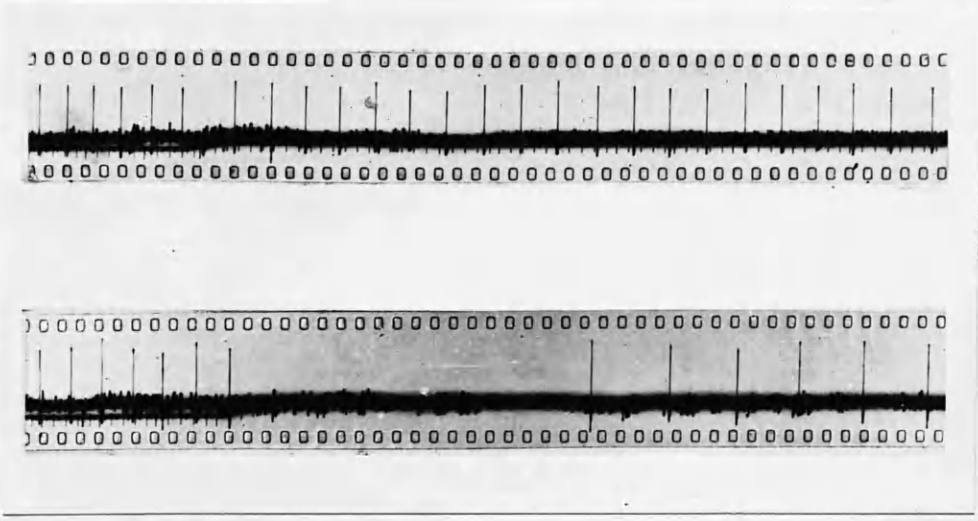



Fig. 32. A) The response during extension of the knee-joint through 2° at 16°/sec obtained from a unit which gave an increase in impulse-frequency on flexion. There is a steady initial discharge, a fall in impulse-frequency during the movement, and the discharge then 'picks up' to a new, steady value. (Prep. 54)

B) The response of the same unit to 4° of extension of the joint, starting from the same position. The initial frequency is the same as before, but the response now includes a 'silent period' (see text). (Prep. 54)

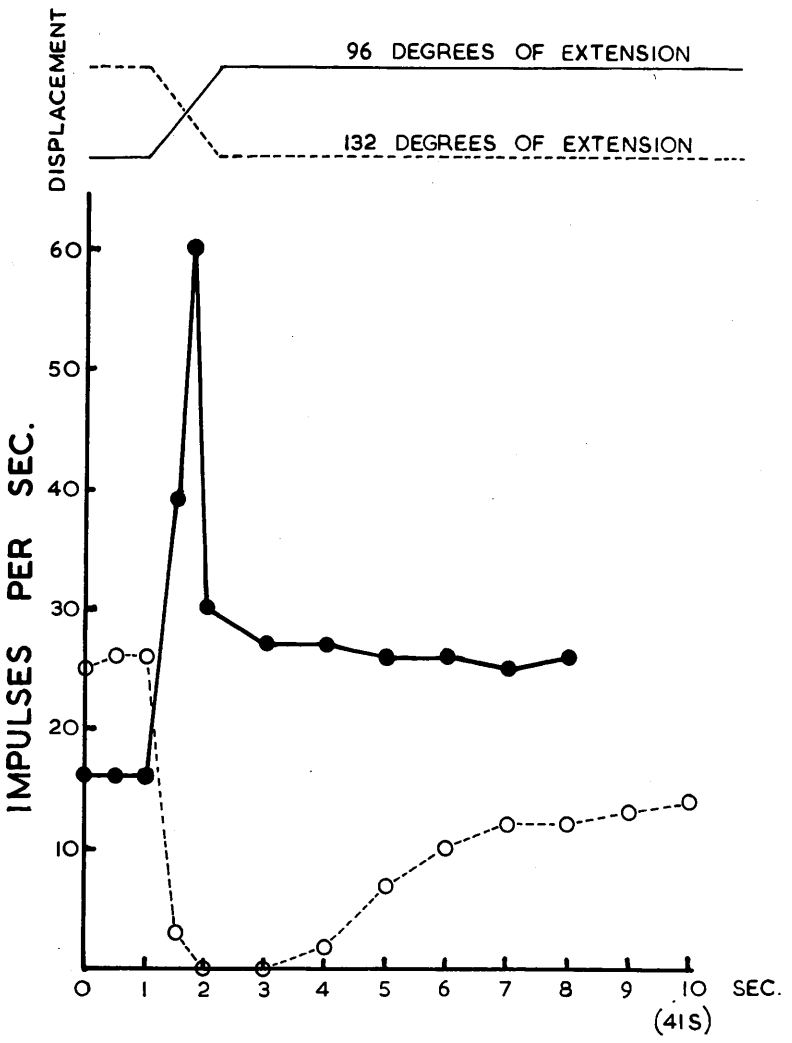



Fig. 33. Graph of the response of a slowly-adapting sensory unit to two movements in opposite directions between the same two positions. The corresponding displacements are shown above. (Prep. 52.)

frequency change being greater than that required to reach the steady value appropriate to the new position.

The effect of a movement producing a decrease in impulse-frequency is shown in Fig.32. The 'exaggeration' process occurs here as well, the impulse-frequency falling sharply and then climbing up to a steady value. Fig.33A shows the effect of a very small movement of this kind - there is a sudden fall in the impulse-frequency after which it 'picks up' again to a new level. The same effect may be observed with a larger movement which, however, produces only a small change in the degree of stimulation of the sensory unit e.g. the inverted response in Fig.30D. Usually a movement in the direction producing a decrease in impulse-frequency produces an actual stopping of the discharge, as shown in Fig.32B, a record similar to Fig.32A, but in which the movement has been one of slightly greater amplitude. The period in which there is no discharge is referred to as the 'silent period'.

These points may be further illustrated by reference to Figs.33 & 34. In Fig.33 the full line indicates the response of a sensory unit to flexion of the joint, starting from a position in which there is already a steady discharge. The broken line shows the response to

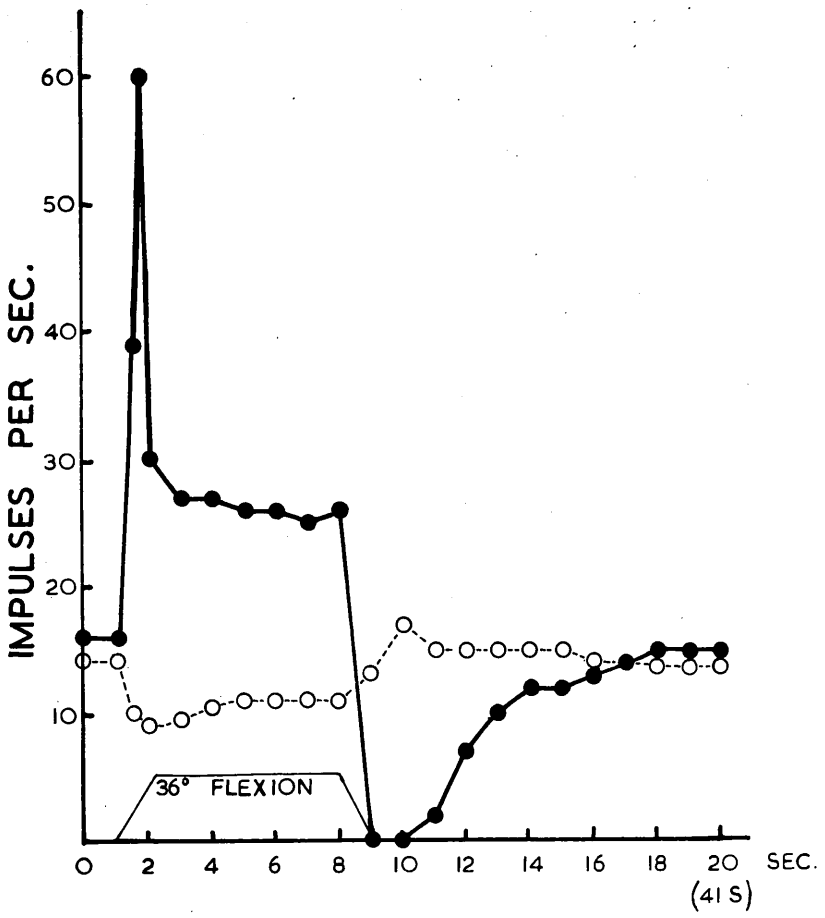



Fig. 34. Graph of the responses of two slowly-adapting units during a movement through 36° (flexion) at 30°/sec, and back again. The impulses were recorded from the same nerve-twig (see fig. 30D). Note that the changes in impulse-frequency are in opposite senses and that each unit returns to its original frequency of discharge. (Prep. 52.)

the return movement of extension - there is an exaggeration of the frequency change which includes a silent period of 1 sec. The first part of the broken curve in fig.34 illustrates the fact that where the change in steady frequency due to a movement is small, i.e. there is little change in the degree of stimulation of the sensory unit, there is little exaggeration and no silent period.

After a movement in the direction producing a decrease in the impulse-frequency the time taken for the response to 'pick up' to its steady level is considerably longer than that required when adaptation is taking place down to the steady value. The time taken is usually more than 10 secs and is often as much as $\frac{1}{2}$ min. The response indicated by the broken line in Fig.33 took 15 secs to attain its final level of 16 impulses/sec (not shown). The time required for the process depends, as in the case when the final level is approached from above, on the velocity of the movement and on the change in the value of the steady frequencies in the initial and final positions. This latter fact is illustrated by the broken curve of Fig.34 where the change in steady frequency is only 3 impulses per sec and the final level is reached in 4 secs.

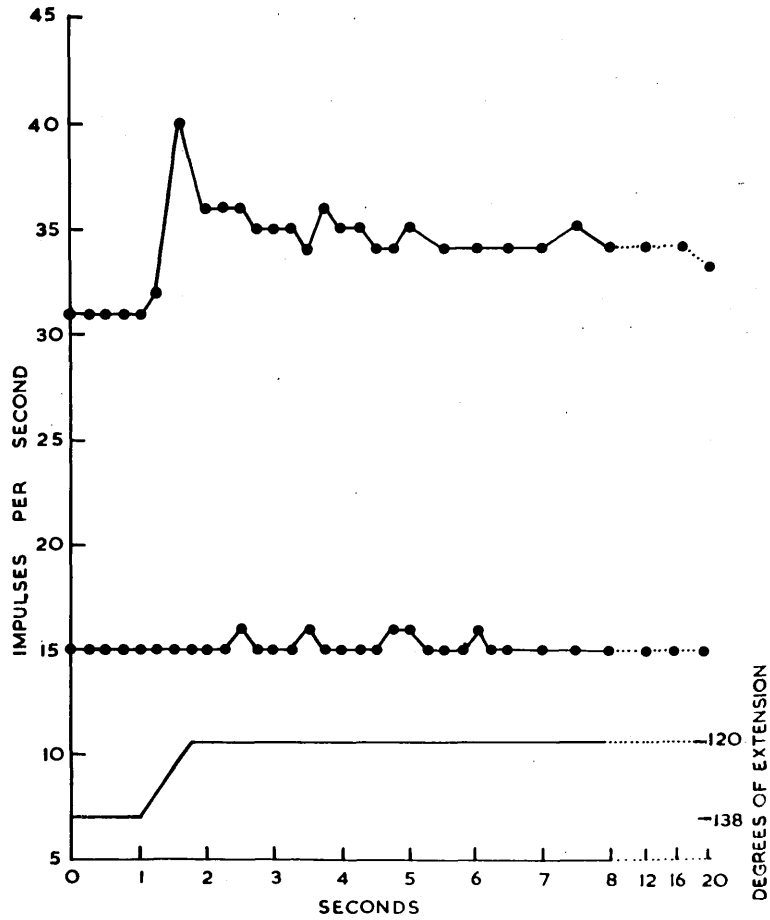



Fig. 35. Graph of the responses of two sensory units during a movement of flexion as shown by the thin line. The impulses were recorded from the same nerve-twig. Note that one unit responds with an increase in impulse-frequency followed by the usual process of adaptation, but the second unit shows no change in impulse-frequency other than the minor fluctuations which normally occur in the steady value of the impulse-frequency when the joint is maintained in any one position. (Prep. 73.)

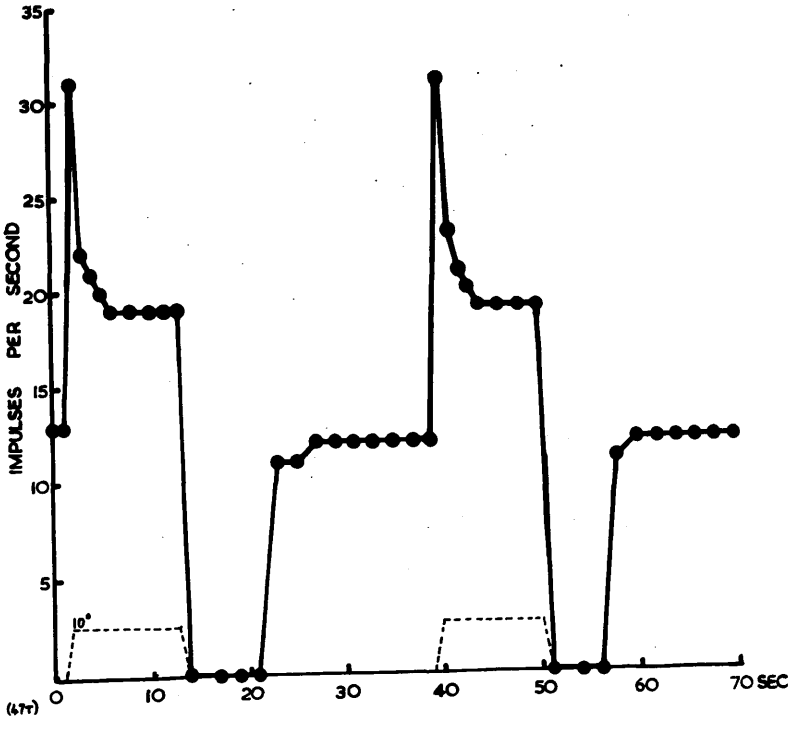



Fig. 36. Graph of the response of a single unit during a repeated movement through 10° (flexion) at 16°/sec and back again, as indicated by the dotted line. Note the similarities in steady frequencies and in the courses of the adaptation curves. (Prep. 54.)

In Fig.34 are shown the responses of the two units in Fig.30D during a movement from one position to another and back again. The continuous curve corresponds to the spikes which are directed upwards, and the broken curve to those directed downwards. The differing behaviour of the two units is clearly demonstrated, as is also the fact that in this case each unit has a specific steady frequency of discharge for each position. The fact that units may respond in a different way to the same movement is further illustrated in Fig.35. Here, again, the responses of two units were recorded from the same twig during a movement of flexion of the knee, and while one of the units shows an increase in impulse-frequency, the other shows no change in frequency other than the minor variations that occur normally in the steady value in any position.

If a movement between two positions is repeated at the same rate, similar adaptation curves and similar final steady impulse-frequencies are obtained, as shown in Fig.36. The steady discharges may be maintained over long periods. This is shown by the frequency of the occasions on which discharges were encountered in nerve-twigs when they were first placed over the electrodes, even when the joint had been stationary for an hour or two previously. Further, the same unit has on some occasions

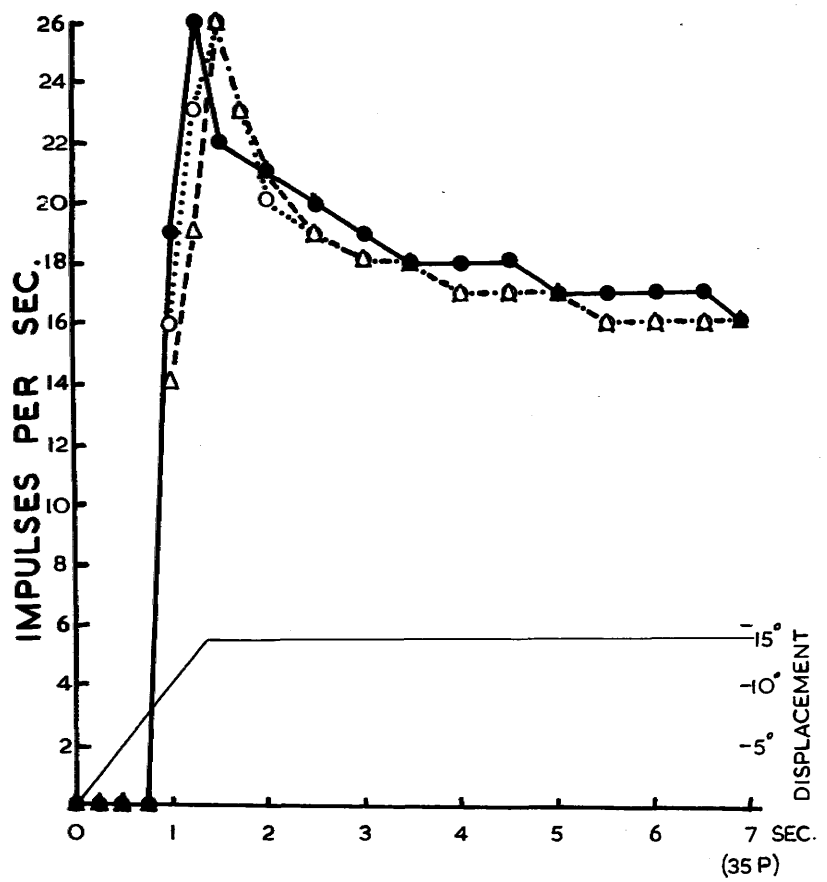



Fig. 37. Graph of the responses of a single unit during three similar movements from the same starting position, each through 14° (flexion) at 10°/sec. The displacement is indicated by the thin full line. The continuous curve was obtained some 15 min before the other two. (Prep. 50, unit C.)

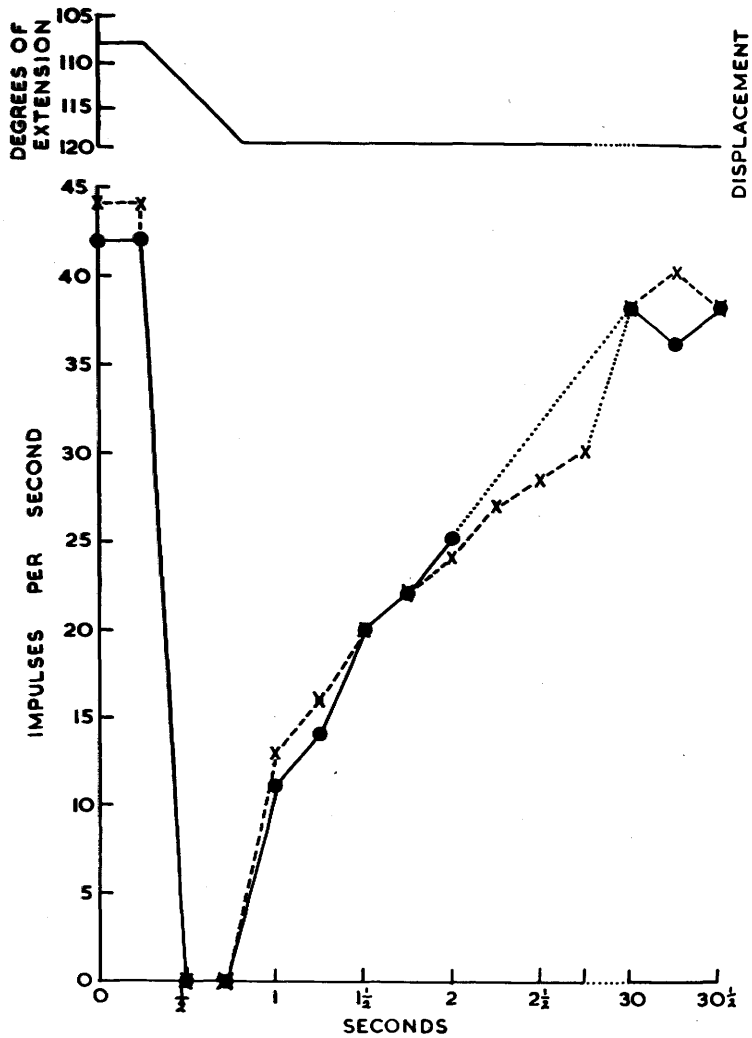



**Fig. 38.** Graph of the responses of a unit, which gave an increase in impulse-frequency on flexion, during two similar movements of extension as shown by the thin full line above. The broken curve was obtained ½ hr after the full one, and yet the curves are almost the same.

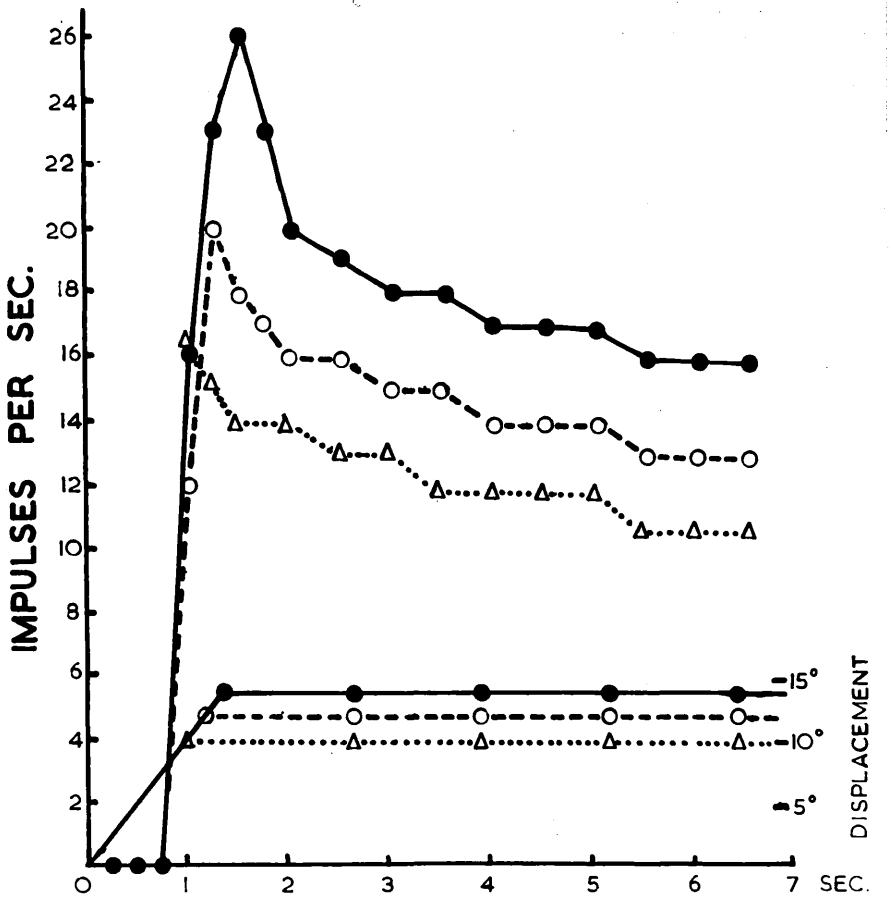



Fig. 39. Graphs of the responses of a single unit during flexion at 10°/sec through three different angles from the same starting position. The upper curves show the frequencies of the impulses, the lower ones the angular displacements from a position of 132° of extension where this unit did not discharge. (Prep. 50, unit C.)

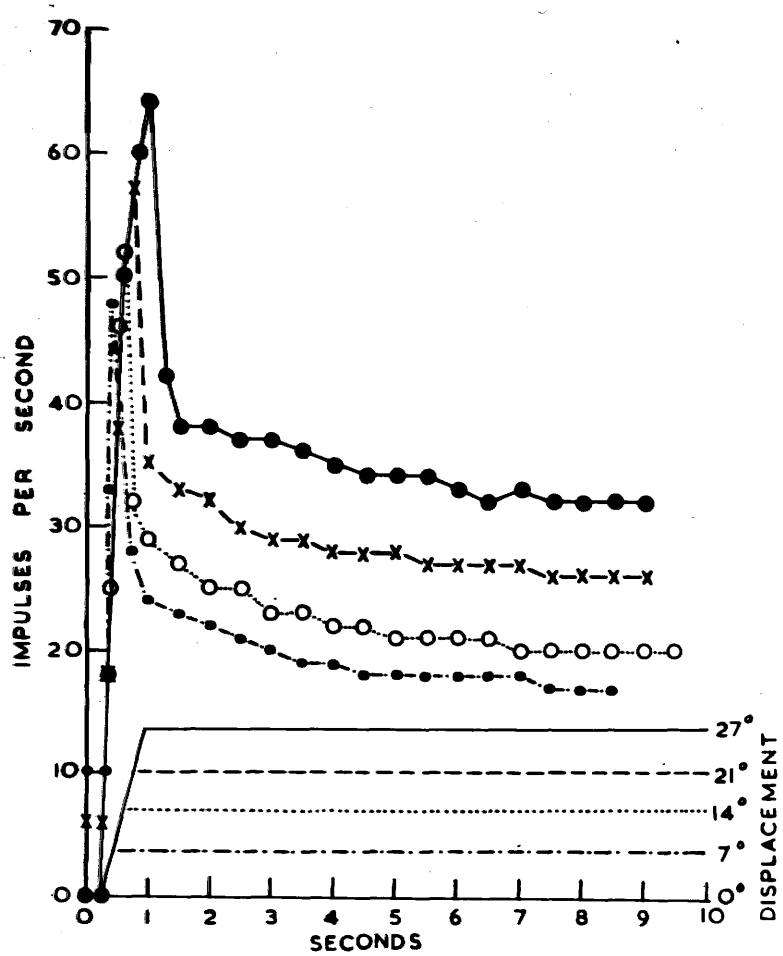



Fig. 40. Graphs of the responses of a single unit during outward twisting of the tibia at 34° per sec through four different angles. The upper curves show the frequencies of the impulses, the lower ones the angular displacements. (Prep. 40, unit A.)

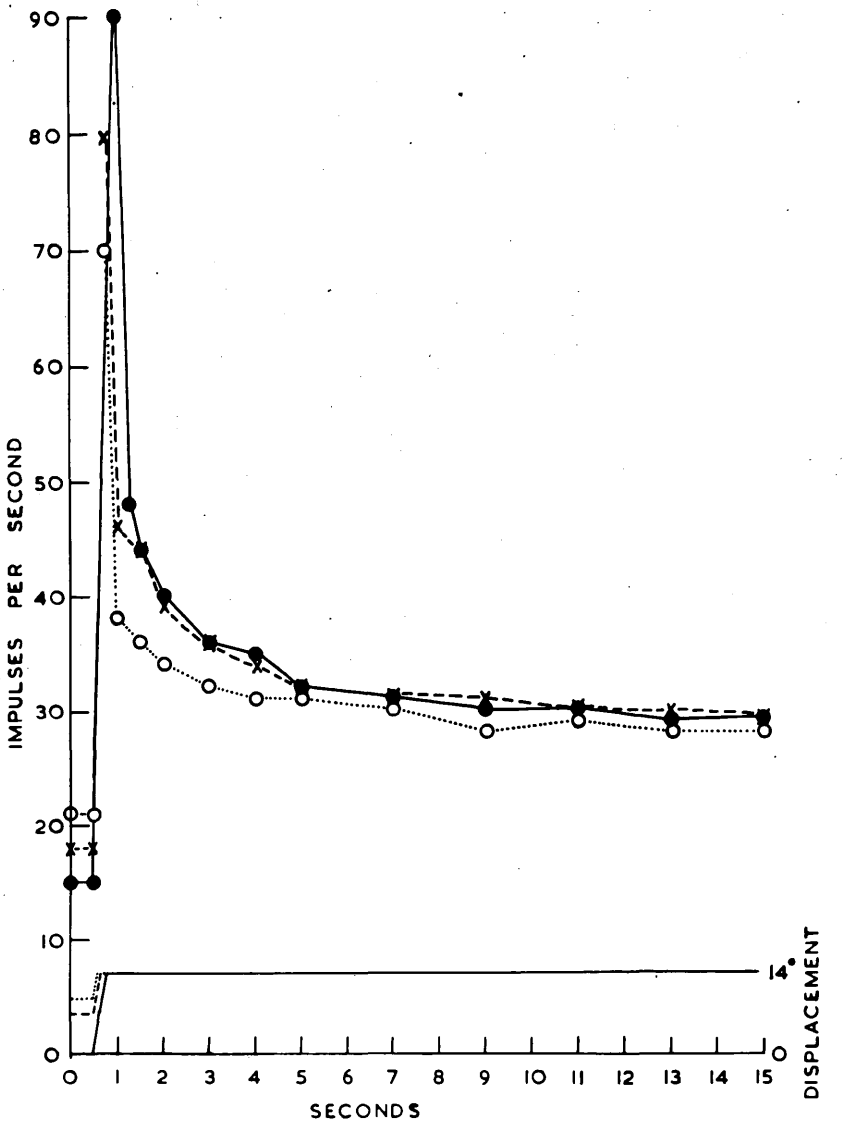



Fig. 41. Graphs of the responses of a single unit to outward twisting of the tibia at 30°/sec through three different angles (●, 14°; X, 7°; O, 4°) finishing in the same position. The initial frequencies are different but the final frequencies are almost the same. (Prep. 60)

been maintained in contact with the electrodes for up to 5 hr without moving the joint, and the discharge continued during this period. Measurements made at intervals showed that the frequency varied by less than 2-3 impulses per sec. On no occasion has a discharge been observed to stop after continuing unchanged for several minutes.

The striking similarity in the response to a particular movement carried out at different times is further illustrated by Fig.37, in which the continuous curve was obtained some 15 min before the other two, and in Fig.38 where the broken curve was obtained $\frac{1}{2}$ hr after the full one.

The response of the same unit to flexion at the same rate, from the same starting position, through different angles, is illustrated in Fig.39. The steady impulse-frequencies ultimately reached and the courses of the adaptation curves were quite distinct, although the final positions were only $2^{\circ}$ apart. The same result for four twisting movements is shown in Fig.40. Fig.41 shows the effect of moving at the same rate, to the same final position, starting from three different positions. Here the initial impulse-frequencies are different, but the final frequencies are almost the same. Again there

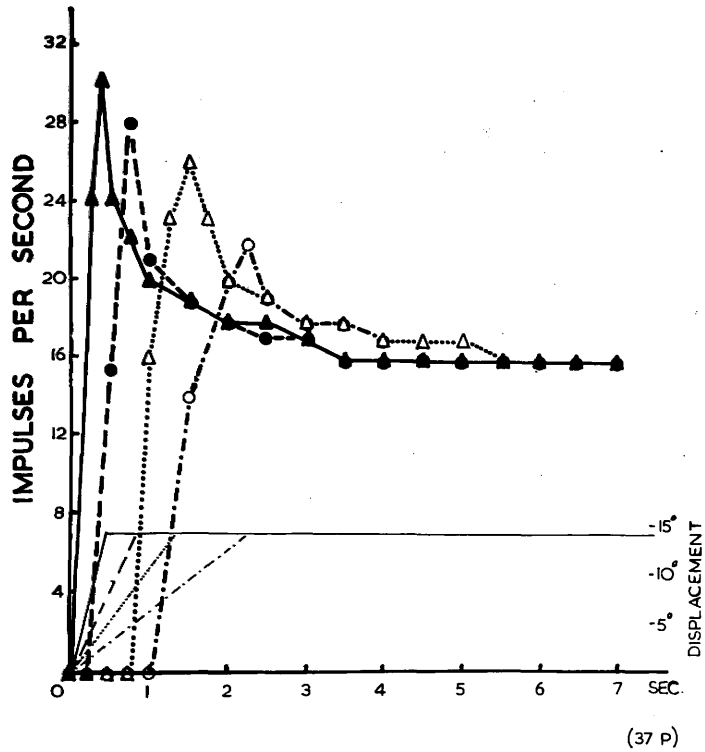



Fig. 42. Graphs of the responses of a single unit during movements of flexion between the same positions at four different rates: ▲, 35°/sec; ●, 17°/sec; △, 10°/sec; ○, 6°/sec. The displacements are indicated by the thin lines. Note that the steady impulse-frequency in the final position is the same in each case. (Prep. 50, unit C.)

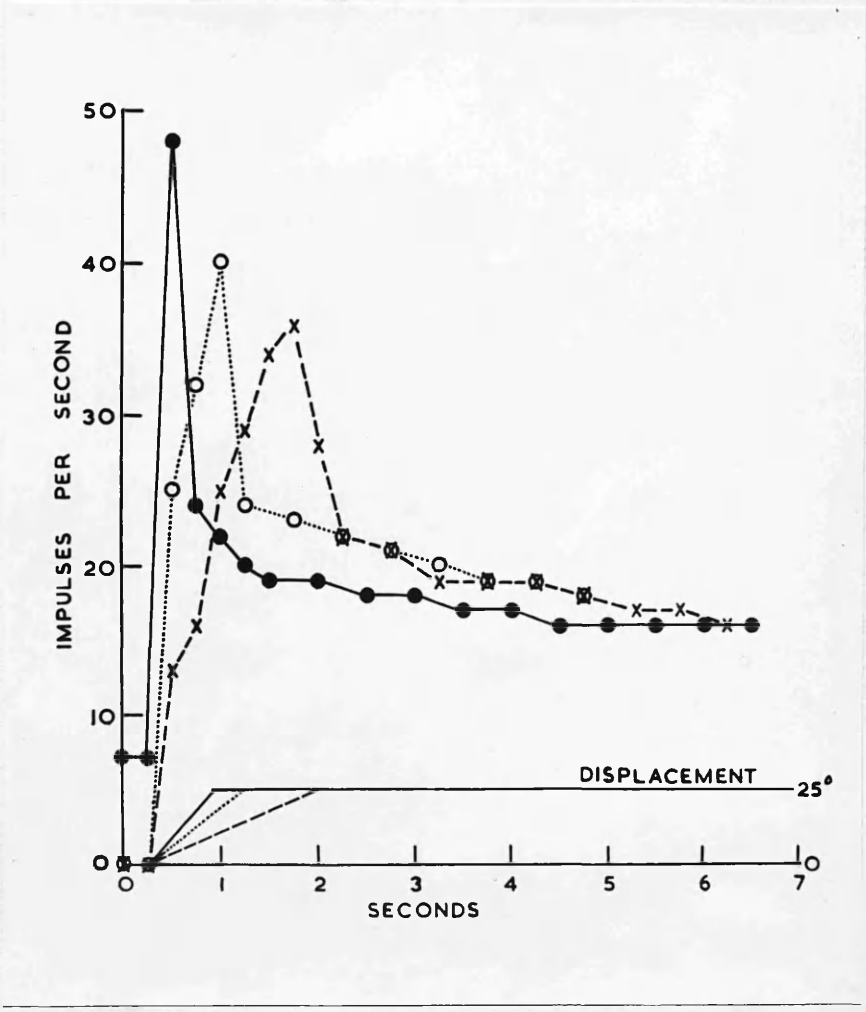



Fig. 43. Graphs of the responses of a single unit during movements of 25° of outward twisting of the tibia at three different rates: ●, 50°/sec; O, 30°/sec; X, 15°/sec. The displacements are indicated by the thin lines. Note that the final impulse-frequency is the same in each case. (Prep. 40, unit A.)

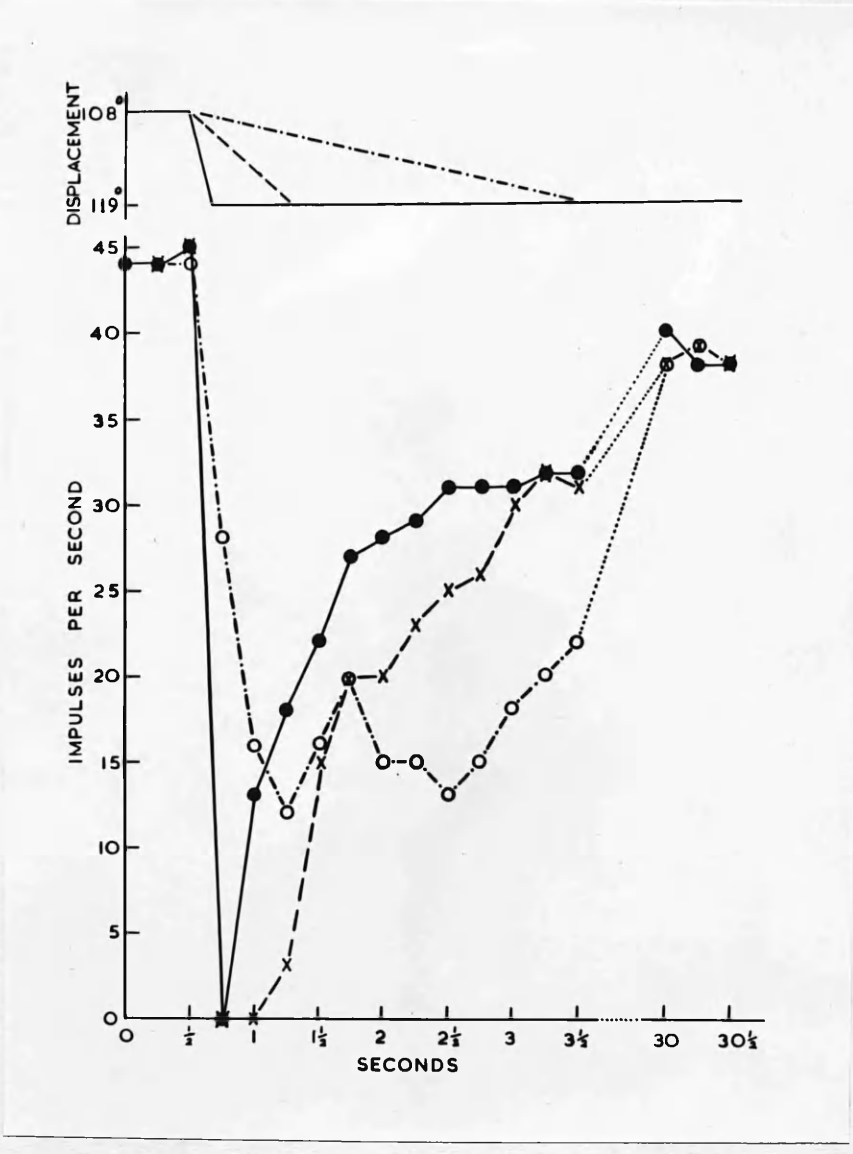



Fig. 44. Graphs of the responses of a single unit, which showed an increase in impulse-frequency during flexion, to movements of extension between the same positions at three different rates, as shown by the displacement curves above. Note that the initial and final frequencies are the same. (Prep. 64.)

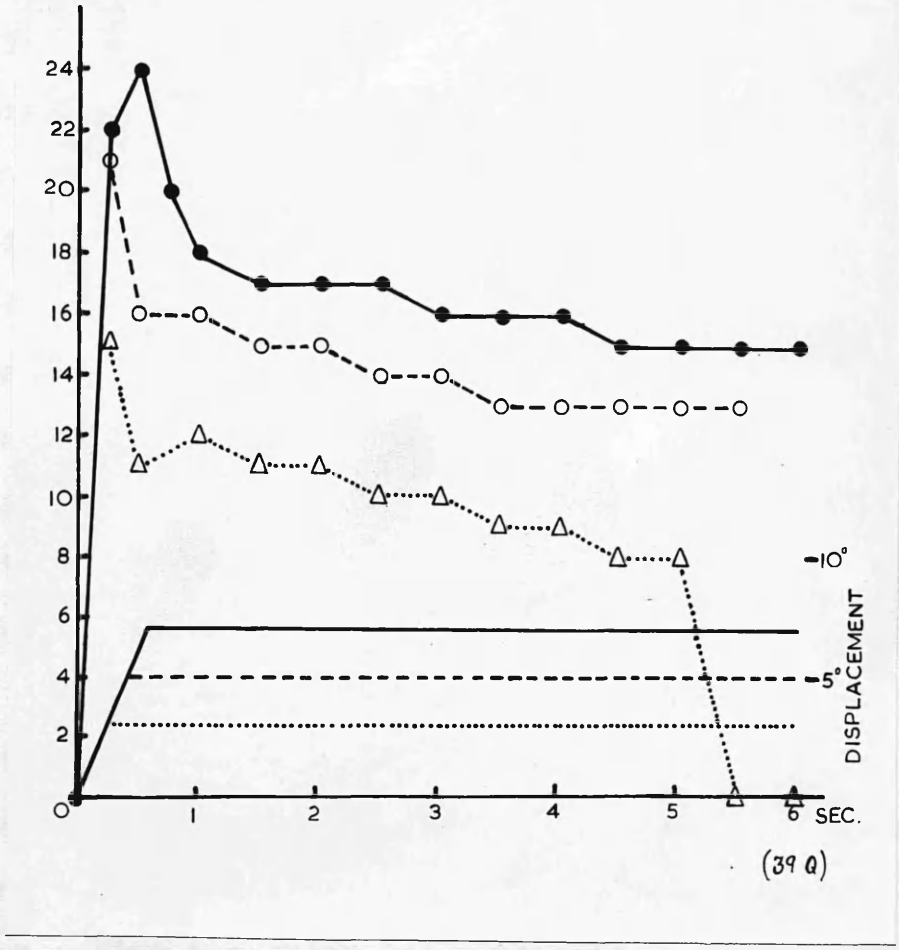



Fig. 45. Graphs of the responses of a single unit during extension at 12°/sec from the same position through three different angles: ● , 7°; O , 5°; △, 3°. The full and broken lines below the response curves indicate the corresponding displacements. Where the displacement is only 3° the discharge is not maintained. (Prep. 50, unit B.)

appears to be a definite relation between the position of the joint and the fully adapted frequency in that position.

The effect of moving through the same angle at different rates is shown in Figs 42, 43, & 44. Fig.42 shows the effect of a movement of flexion between two positions at four different rates. The peak frequency is greater with more rapid movement, but the steady frequency for the final position is the same in each case. The same result for twisting movements is shown in Fig.43. In Fig.44 is shown the effect of movement, in the direction producing a decrease in impulse-frequency, between the same positions, at three different rates. Here, again, the initial and final frequencies are the same in each case, and the degree of exaggeration depends on the rate of movement - during the slowest of the three movements the impulse-frequency does not fall to zero, as it does during the other two movements.

Occasionally discharges were observed which, after some adaptation, stopped altogether, only a few seconds after the end of the movement (e.g.Fig.30B). In such cases, however, it was usually possible, by a larger movement, to produce a maintained discharge. This is illustrated in Fig.45; where the amplitude of the

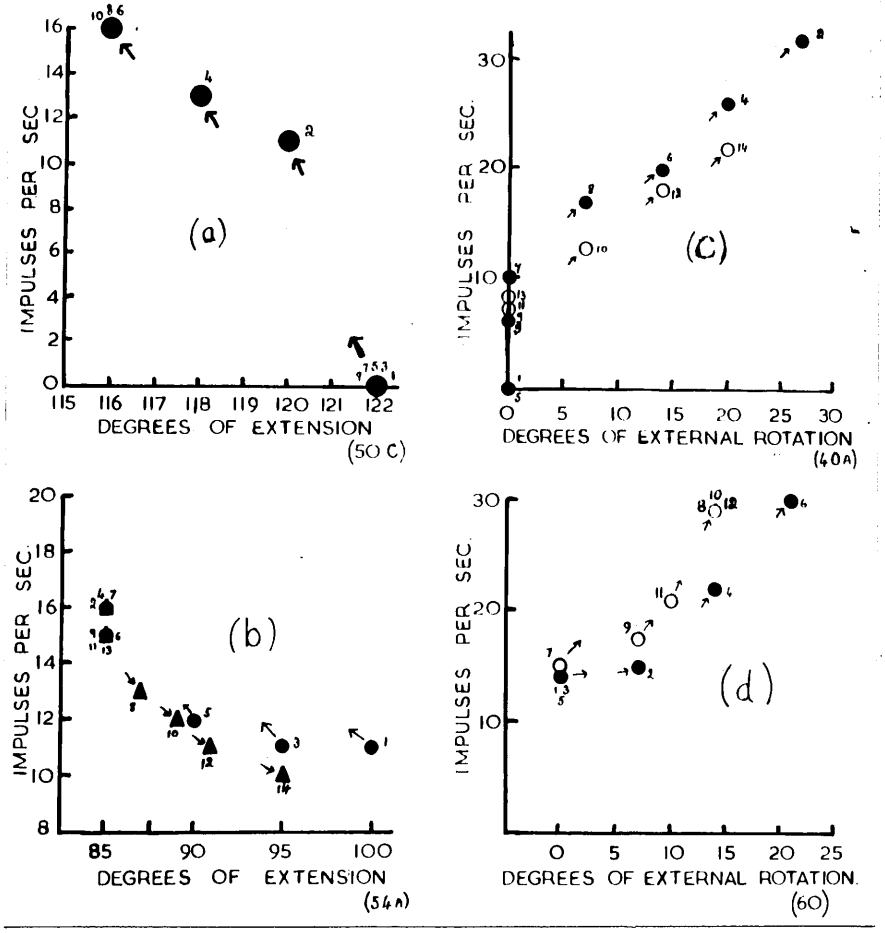



**Fig. 46.** The relation between impulse-frequency and position for four different slowly-adapting sensory units. The points represent the steady impulse-frequencies at the beginning and end of a number of movements. The order in which the points were obtained for a particular unit is indicated by the small numbers, and the directions of the movements during which records were taken are shown by the arrows. Where several numbers are associated with one point this shows that the same impulse-frequency was observed in the indicated position on several occasions.

a) A unit responding with increased frequency on flexion of the knee. The values plotted are also shown in Figs. 37 & 39. The values from Fig. 42 might also have been included. (Prep. 50, unit C.)

b) A unit responding with increased frequency on flexion of the knee. ●, readings obtained at the start and finish of three movements of flexion; ▲, readings for four movements of extension. (Prep. 54.)

c) and d) Units responding with increased discharge on outward twisting of the tibia. In each case the two sets of observations, indicated by the filled and open circles, were made at different times. (c, prep. 40; d, prep. 60.)

movement was only $3^{o}$ the discharge slowed and stopped completely; where the amplitude was $5^{o}$ or more adaptation occured to a steady value which was maintained. It appears that if the adaptation curve is of such a form as would lead one to expect a steady frequency of less than about 10 impulses per sec as appropriate to the new position, then the discharge usually becomes irregular and stops within a few seconds.

Stimulus - response relationship.

If the values of the steady, adapted impulse-frequency at the beginning and end of a number of movements are observed for a single sensory unit, a graph may be plotted between position and adapted impulse-frequency. Graphs of this kind for four different units are shown in Fig.46. The points indicate the steady impulse-frequencies before and after movement between various positions. The order in which the positions were reached is indicated by the small numbers beside the various points, and the arrows indicate the directions of the movements during which records were taken. Many of the points represent repeated observations. Different symbols on the one graph indicate different sets of readings obtained with the same unit. The apparent discrepancies between the two sets of points in each of the figures for twisting movements can be

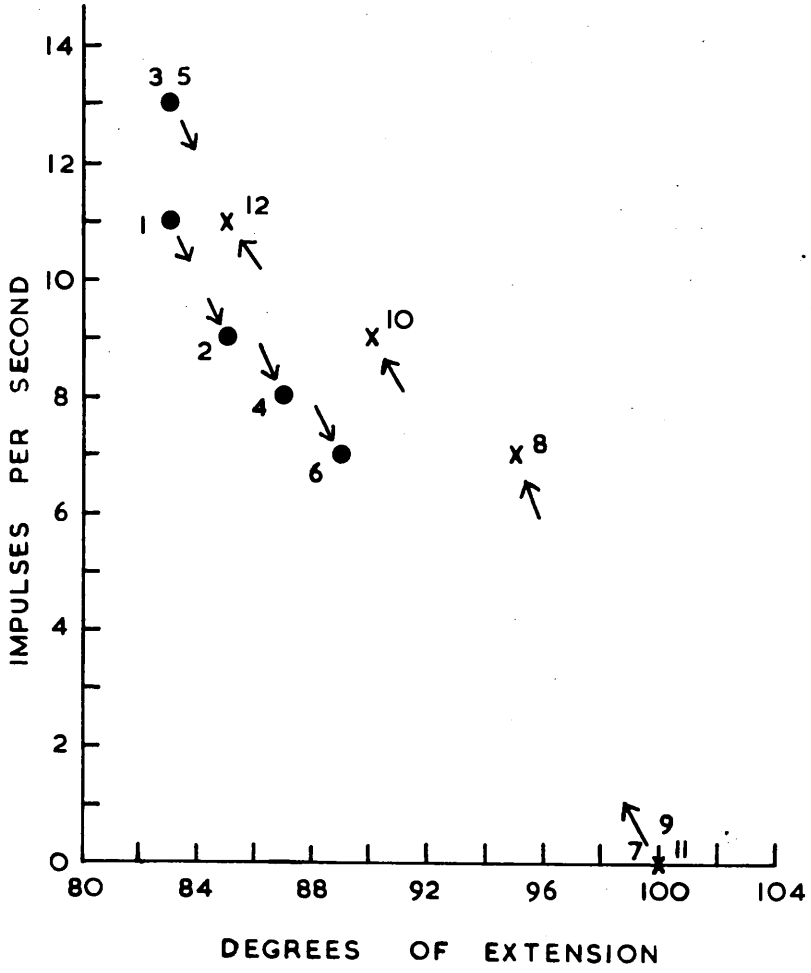



Fig. 47. The relation between impulse-frequency and position for a slowly-adapting sensory unit. The circles represent the values of the adapted impulse-frequency at the beginning and end of three movements of extension; the crosses represent the values at the beginning and end of three movements of flexion. The notation is the same as in fig. 46. Note that the adapted impulse-frequency in the position of 85° of extension when the position was reached by a flexion movement differs from the value when the position was reached by an extension movement. (Prep. 56.)

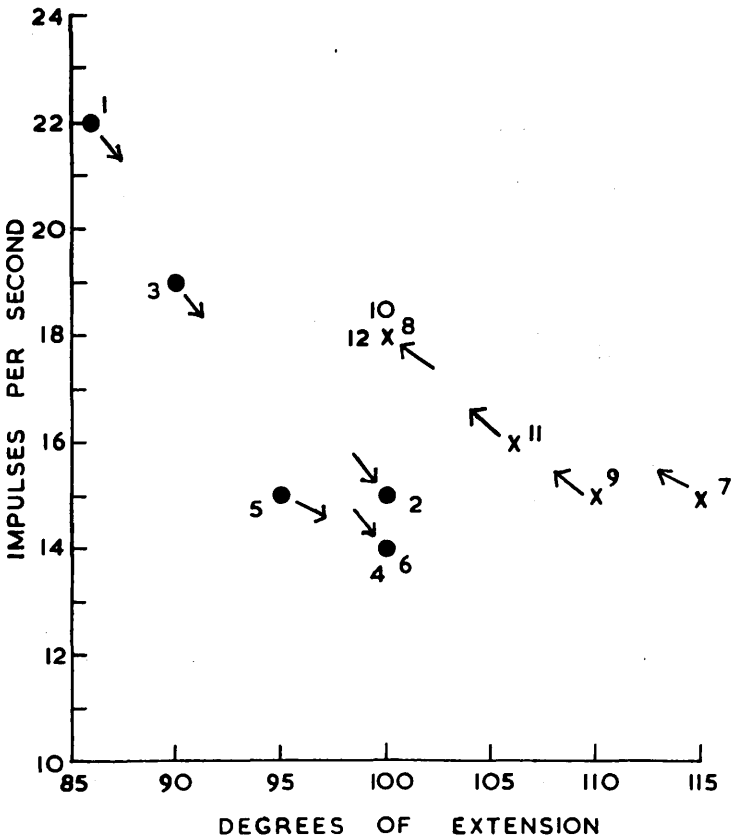



Fig. 48. The relation between impulse-frequency and position for a slowly-adapting sensory unit. The circles represent the values of the adapted impulse-frequency at the beginning and end of three movements of extension; the crosses represent the values at the beginning and end of three movements of flexion. The notation is the same as in fig. 46. Note that the adapted impulse-frequency in the position of 100° of extension when the position is reached by flexion movements differs from the value when the position was reached by movements of extension. (Prep. 52, unit A.)

ascribed to the fact that the position taken as zero may have been slightly different in the two sets of observations.

The relation between adapted frequency and position for two other units is shown in figs. 47 & 48. The filled circles in fig. 47 represent the values of adapted frequency before and after movements of extension from one position to three different positions. The crosses are the values before and after three movements of flexion. In this case the adapted frequency in the position of 85° of extension was different when the position was approached from opposite directions (9 impulses per sec after extension; 11 impulses per sec after flexion). In fig.48 are shown the values of the adapted impulse-frequency (from another unit) in the position of 100° of extension, when this position was reached by three movements of flexion of different amplitude, and three of extension, all at the same rate. After each of the flexion movements the value was 18 impulses per sec; after the extension movements the value was 14 or 15 impulses per sec. The discrepancy, shown by these units, between the values of the adapted frequency in a particular position when this position was approached from opposite directions will be discussed later.

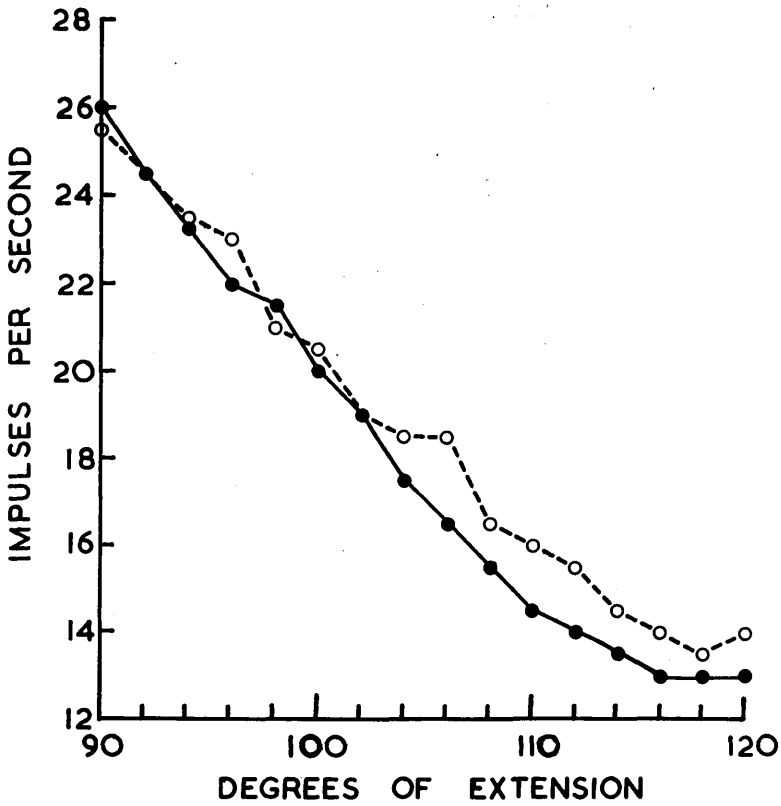



Fig. 49. Graph of the relation between steady, adapted impulse-frequency and position of the joint for a slowly-adapting sensory unit. The values connected by the full line were obtained as direct readings on the pulse-interval meter after successive steps of 2° of flexion; those connected by the broken line were obtained after similar steps of extension of the knee-joint. Note that the values of the impulse-frequency after flexion and after extension of the joint to any one position are almost the same. (Prep. 82, unit B.)

It was obvious that to establish the relation between joint position and impulse-frequency with any certainty for any one sensory unit, many more points would be required for the graph. This was achieved using the pulse-interval meter, the impulse-frequency in any position being read directly off the meter, photographic recording and measurements of pulse-intervals on films being unnecessary. Examples of the relation between position of the joint and adapted impulse-frequency for a number of slowly-adapting units are shown in Figs.49-56. The readings connected by the full lines were obtained, in each case, after small steps of movement in the direction producing an increase in the impulse-frequency; those connected by the broken lines were obtained after steps of movement in the direction producing a decrease in the impulse-frequency. In Fig.49 for example, the readings connected by the full line were obtained from a single-fibre preparation by commencing with the joint in a position of 120 degrees of extension, and then flexing the joint in increments of $2^{o}$. The movement was carried out very slowly to produce as little exaggeration of the impulse-frequency as possible, and the joint was kept at rest after each increment of movement until the impulse-frequency, as read directly off the pulse-interval meter, had adapted to a steady value. This value is plotted on

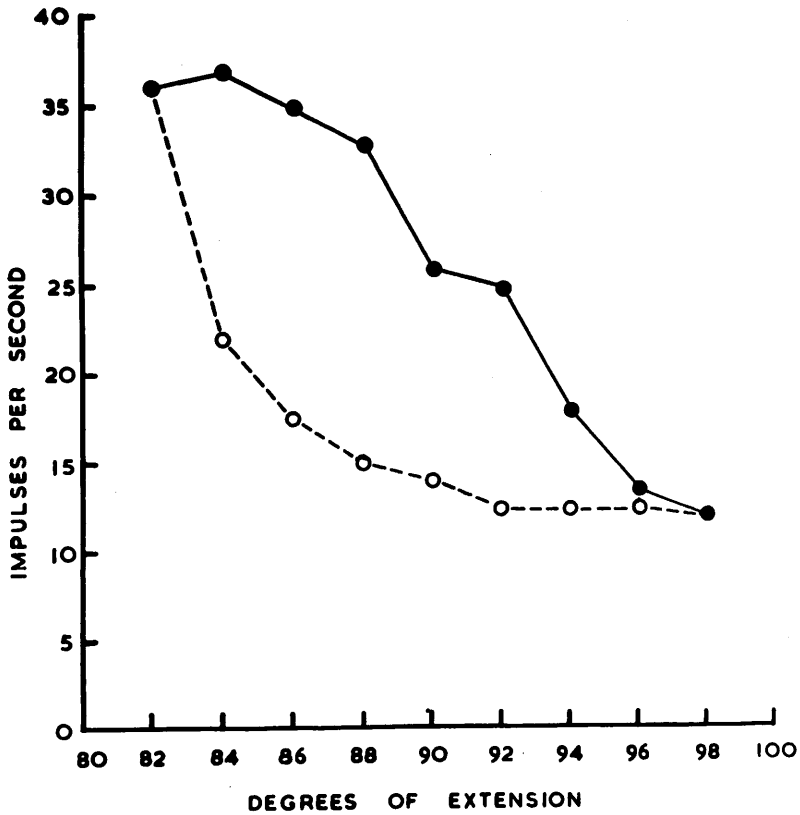



Fig. 50. Graph of the relation between adapted impulse-frequency and position of the joint for a slowly-adapting sensory unit. The readings connected by the full line were obtained after successive steps of 2° of flexion; those connected by the broken line were obtained after similar steps of extension of the joint. Note that, in any one position, the value of the impulse-frequency after a movement of extension to this position is much less than that after flexion to the same position. (Prep. 84.)

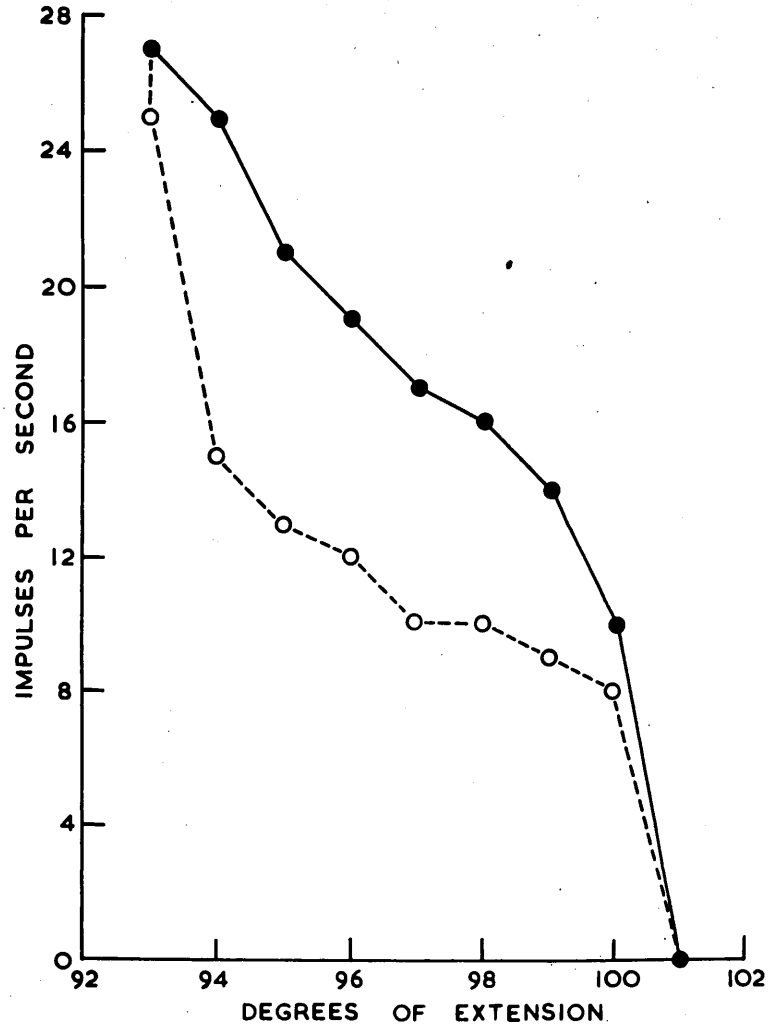



Fig. 51. Graph of the relation between adapted impulse-frequency and position of the joint for a slowly-adapting sensory unit. In any one position the value of the impulse-frequency after a movement of extension to this position is much less than that after flexion to the same position. (Prep. 97).

the graph against the corresponding position. The readings connected by the broken line were obtained during increments of extension, readings being taken in the same positions as before. It will be seen that the adapted frequency in any one position is almost specific for that position, there being not more than 2 impulses per sec, and often less than 1 impulse per sec, difference in the frequency given by the two curves when the joint was in any one position.

Detailed study of the response of a considerable number of sensory units has, however, shown that not all the slowly-adapting units behave in the way described above. While all of them show the position-frequency specificity when the positions are approached in the same direction, e.g. by flexion, the value is not always the same when the position is reached from opposite directions (cf. figs. 47 & 48). Examples of this are shown in figs. 50 & 51 where the readings were obtained in exactly the same way as for fig.49. All the values of impulse-frequency in the various positions after each of the movements of extension are less than those obtained in corresponding positions during flexion. Many sensory units, however, give a response intermediate between the two kinds already described, the difference between the two parts of the cycle being small, but none the less

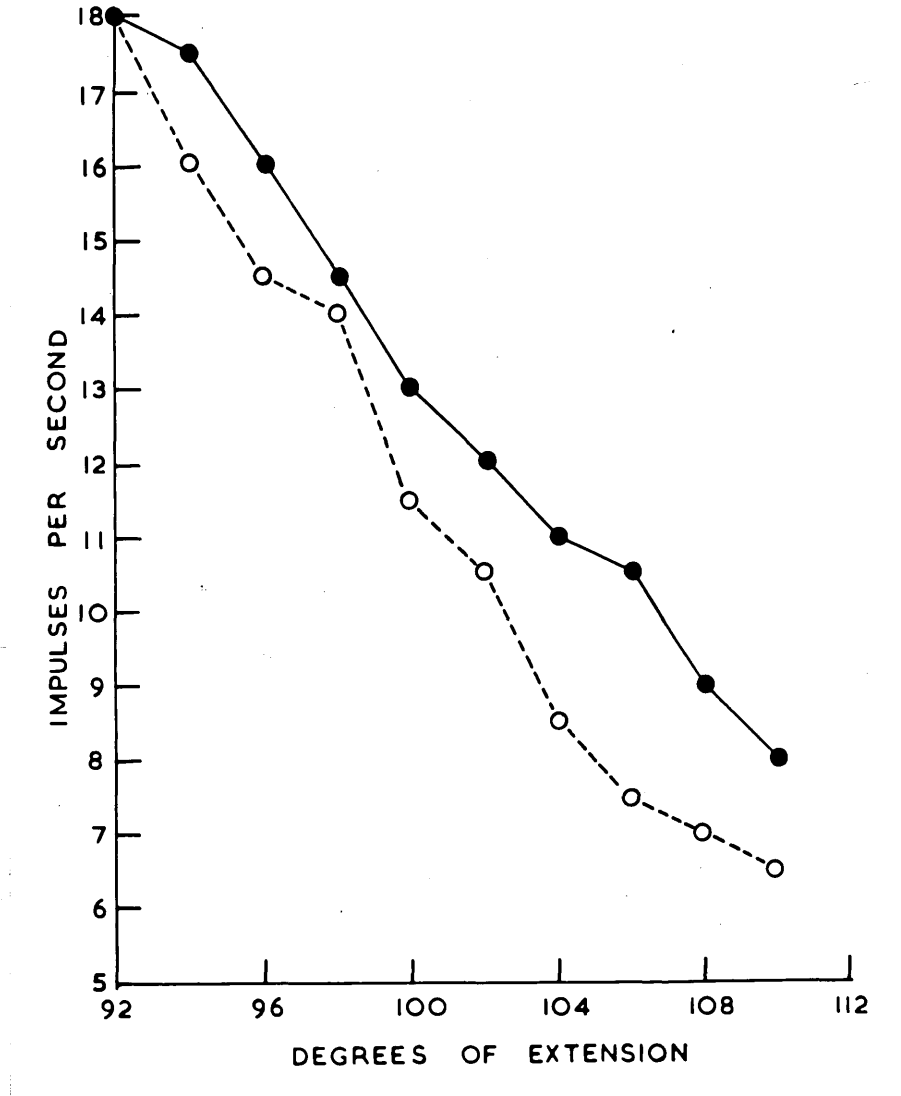



Fig. 52. Graph of the relation between adapted impulse-frequency and position of the joint for a slowly-adapting sensory unit. In any one position the value of the impulse-frequency after a movement of extension to this position is less than that after flexion to the same position. (Prep. 103.)

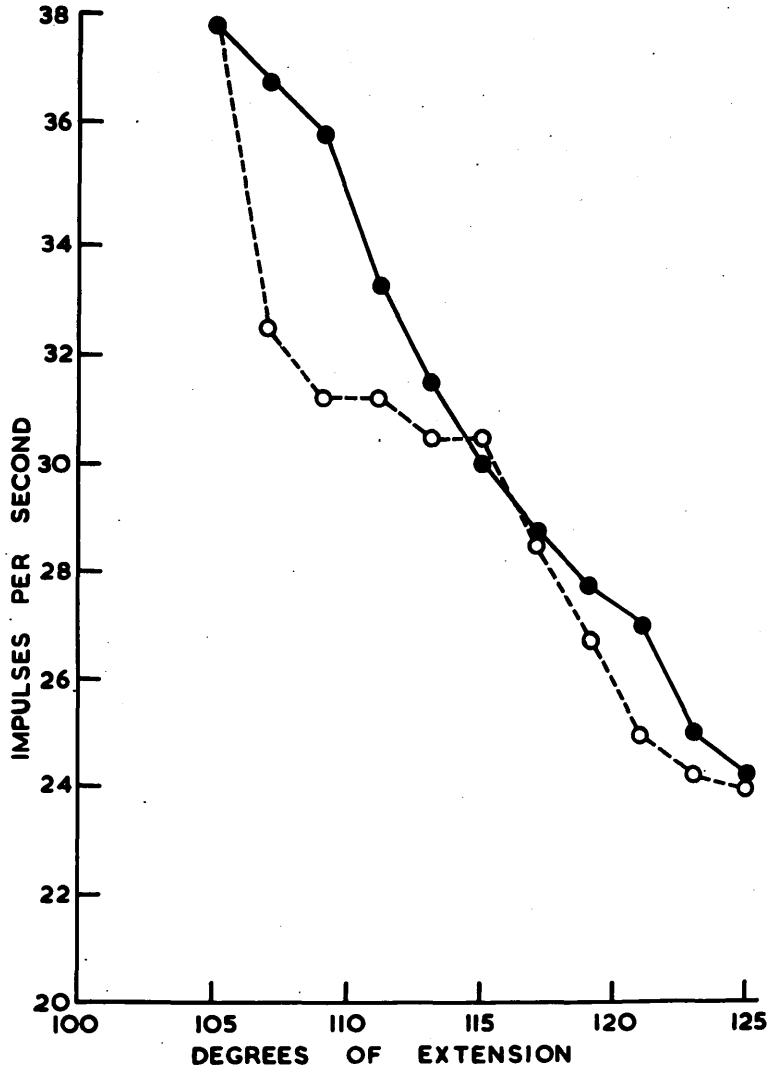



Fig. 53. Graph of the relation between adapted impulse-frequency and position of the joint for a slowly-adapting sensory unit. The values of the impulse-frequency after increments of extension differ from those in corresponding positions after flexion, but the difference varies from position to position and the curves cross in part of their course. (Prep. 87.)

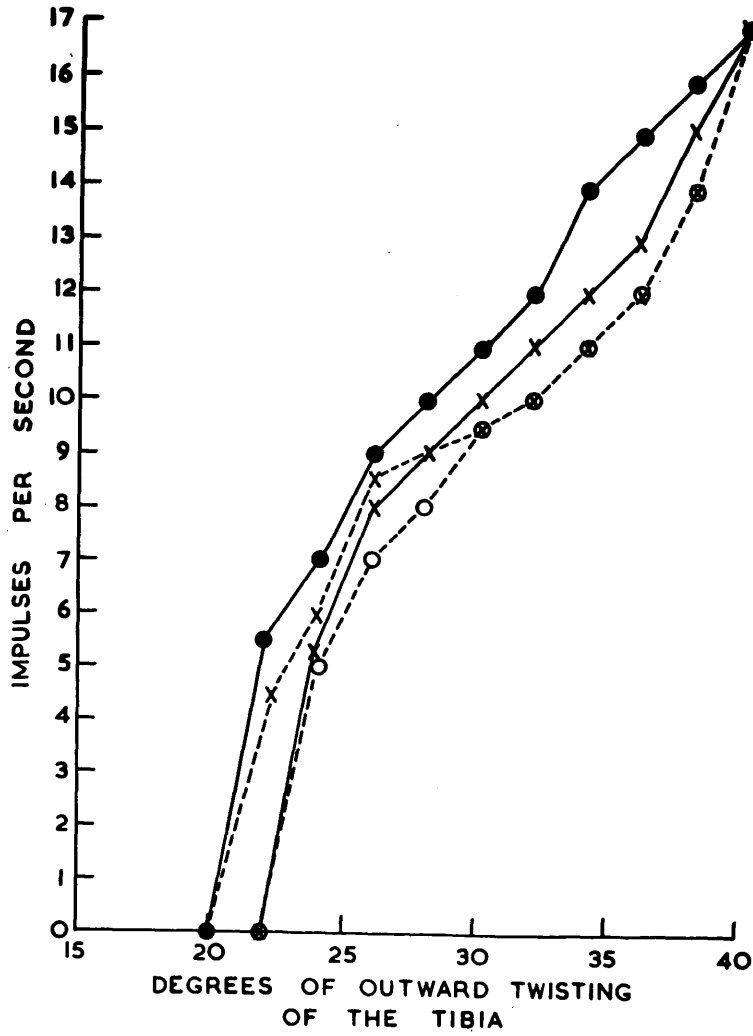



Fig. 54. Graph of the relation between adapted impulse-frequency and position of the joint for a slowly-adapting sensory unit. The values of impulse-frequency were obtained in the usual way, but the cycle of increments of movement was repeated. The two full curves connect the values obtained during the parts of each cycle where movement was in the direction producing an increase in impulse-frequency; the broken curves connect the values during the return movements. The values obtained in the second cycle are not very different from those obtained in the first cycle. (Prep. 107.)

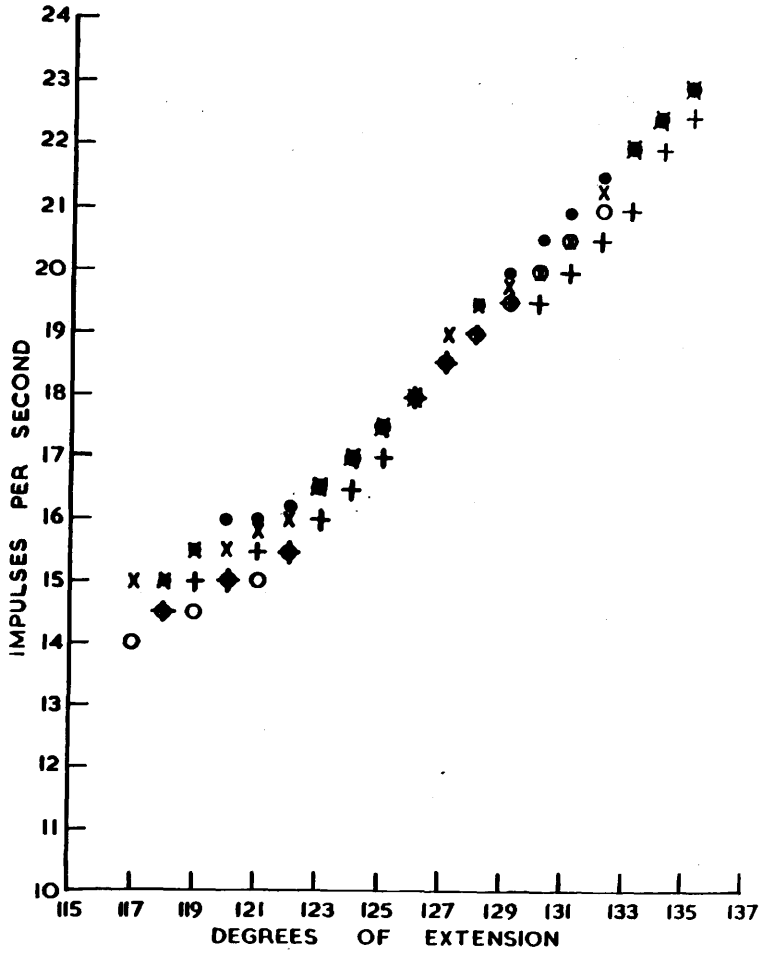



Fig. 55. Graph of the relation between adapted impulse-frequency and position of the joint for a slowly-adapting sensory unit during two cycles of movement carried out as before. The values indicated by the crosses were obtained after steps of 1° of flexion, those indicated by the filled circles after the return steps of extension. The values obtained on repeating the cycle are shown by the empty circles (flexion) and the plus signs (extension). All four values of the adapted impulse- frequency in any one position are within 1 impulse per sec of each other. (Prep. 111.)

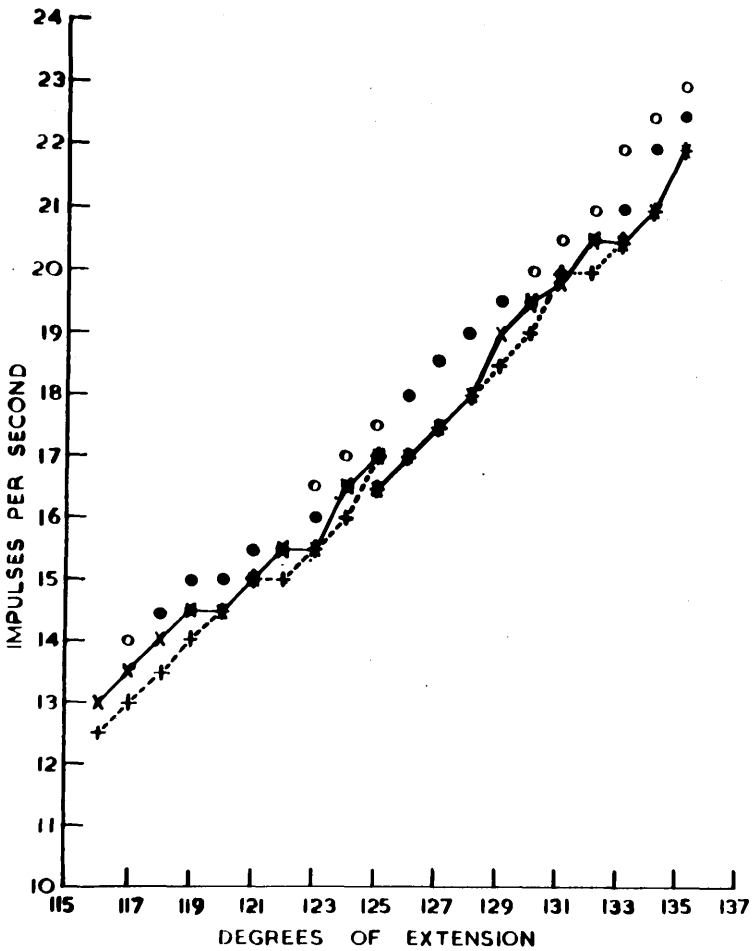



Fig. 56. Graph of the relation between adapted impulse-frequency and position of the joint for the same unit as fig. 55. Values were obtained during two cycles of movement over a smaller range than that of fig. 55. One cycle consisted of steps of extension from 116° - 125° (full line) and back again (broken line); the other was from 125° - 135° (full line) and back again (broken line). Comparable values for a cycle from 137° - 117° and back again are indicated by the empty and filled circles respectively. The values in any position in either of the cycles of smaller amplitude are almost the same as those in the cycle of greater amplitude, even though the smaller cycles were completed about two hours after the larger one. (Prep. 111)

definite. An example is shown in fig.52. Other curves, e.g. fig.53, show differences in the two directions, but the curves cross in part of their course.

When the sequence of movements is repeated, the impulse-frequencies in corresponding positions have almost the same values as in the first sequence. This is shown in fig.54, where the full lines connect the values after the steps of outward twisting of the tibia in the two cycles, and the broken lines the values after the steps of inward twisting. In fig.55 the values indicated by the crosses were obtained after steps of $1^{o}$ of flexion from the position of $135^{o}$, those indicated by the filled circles after the return steps of extension. The values obtained on repeating the cycle are shown by the empty circles (flexion) and the plus signs (extension). All four values of the adapted impulse-frequency in any one position are within one impulse per sec of each other. The effect of carrying out two cycles of movement over a smaller range for the unit of fig.55 is shown in fig.56. One cycle consisted of steps of extension from a position of $116^{o}$ to one of $125^{o}$ of extension (full line) and back again (broken line). The other cycle consisted of steps from $125^{o}$ to $135^{o}$ (full line) and back again (broken curve). Comparable values for steps from $135^{o}$ to $117^{o}$ and back again are indicated by the empty circles and

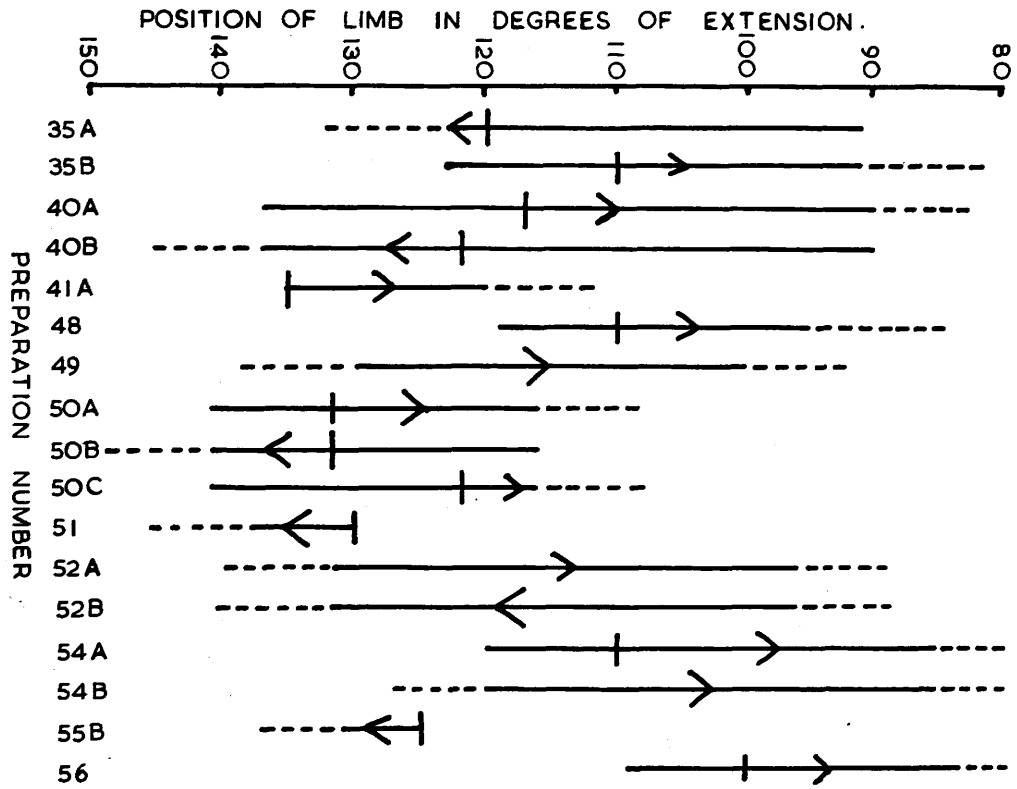



**Fig. 57.** Diagram showing the ranges of flexion and extension (full lines) over which various units were studied. An arrowhead indicates the direction of movement which produced an increase in discharge; the cross-bars show the critical positions (see text); a broken line indicates that part of the range of activity could not be studied owing to the limits of movement imposed by the apparatus.

filled circles respectively. The values in any position in either of the cycles of smaller amplitude are almost the same as those in the same position in the cycle of greater amplitude, even though the smaller cycles of movement were completed about two hours after the larger one.

Active range of movement and critical positions.

The movements of the joint which could be investigated were limited in extent by the experimental arrangement. The electrodes had to be near to the joint as there was only a limited length of nerve available. This, of course, limited the extent of flexion movements as the tibia was brought up against the electrodes. There was also a limit to extension movements as the paraffin spilt out of the pool and left the nerve-twig exposed. Fig.57 indicates by the full lines the ranges of flexion and extension over which various units were studied. The direction of movement producing an increase in impulse-frequency is shown by the arrowhead; the broken lines indicate that the unit must be presumed to act beyond the limits of movement imposed by the experimental procedure.

From figs. 37, 39, 42 it is clear that the discharge from this particular unit does not start at the beginning

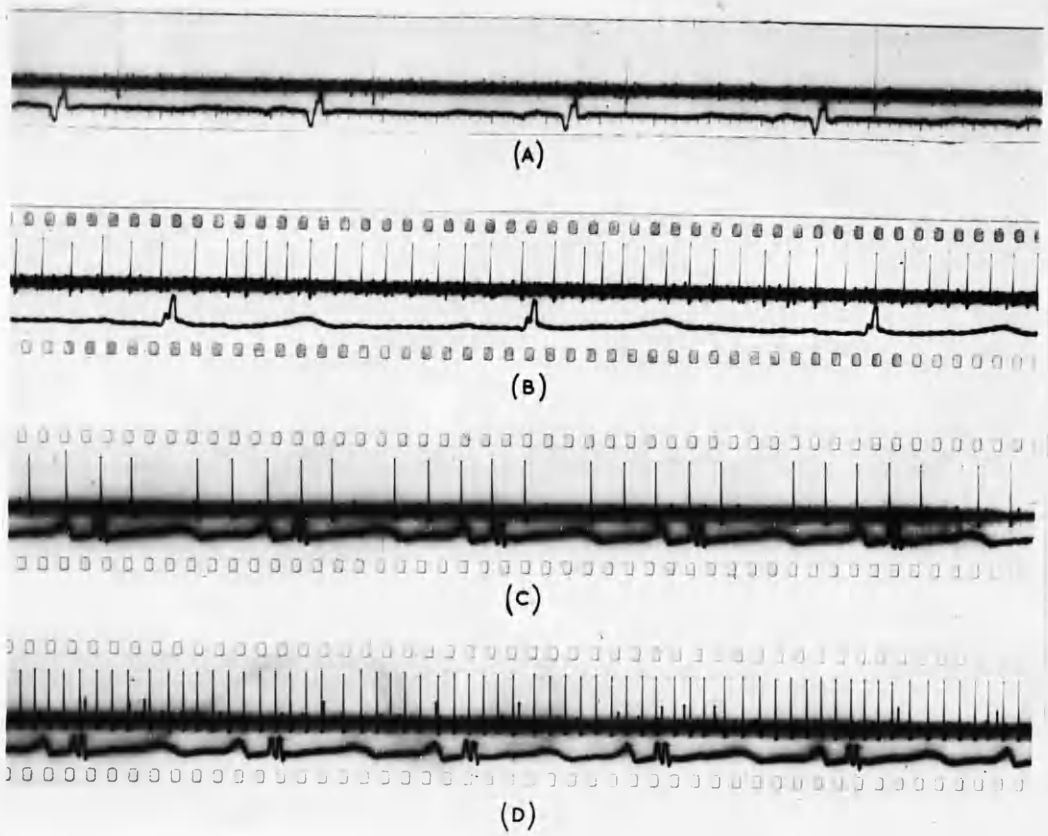



Fig. 58. Records showing the responses of sensory units whic h were affected by the pulse-beat. Signal line = e.c.g.

A) Discharge from a rapidly-adapting sensory unit. A single impulse appears at each pulse-beat. The unit gave an increased discharge during flexion of the knee-joint, and when the movement ceased the response once again fell into step with the pulse-beat. (Prep. 45.)

B) Discharge from a slowly-adapting sensory unit while the knee-joint was held slightly flexed, with the foot turned outwards. The impulse-frequency fluctuates regularly with the pulse-beat (Prep. 61.)

C) Discharge from a slowly-adapting sensory unit. The response fluctuates rhythmically with the pulse-beat. The unit showed an increase in impulse-frequency when the joint was flexed. (Prep. 84.)

D) The response of the unit of (C) after the joint was moved to a position of greater flexion. The response again fluctuates with the pulse-beat, but the average impulse-frequency is higher than before. (Prep. 84).

of the movements. Where the rates of movement are the same (figs. 37 & 39), the discharge starts after the same time interval; where the rates are different (fig.42) the delays are different. This suggests that the critical position is independent of the rate of movement. In fact, the position of 122 degrees of extension was found to be critical for this unit, since discharge always started as this position was passed through, no matter what the rate of movement. Such a critical position was determined for each unit wherever possible, and the critical positions for the units represented in fig.57 are indicated by the cross-bars. No response was obtained from the unit over the range of movement indicated by the continuous line to the side of the cross-bar away from the arrowhead.

It is clear that the ranges covered by individual sensory units show considerable overlapping even amongst units responding in opposite ways, as has already been shown in fig.30D, and in fig.34. The critical positions also show no systematic arrangement.

The response to the pulse-wave.

The response of a number of the sensory units in the knee-joint was found to be influenced by the pulse wave. In fig.58A is shown the response of a unit from

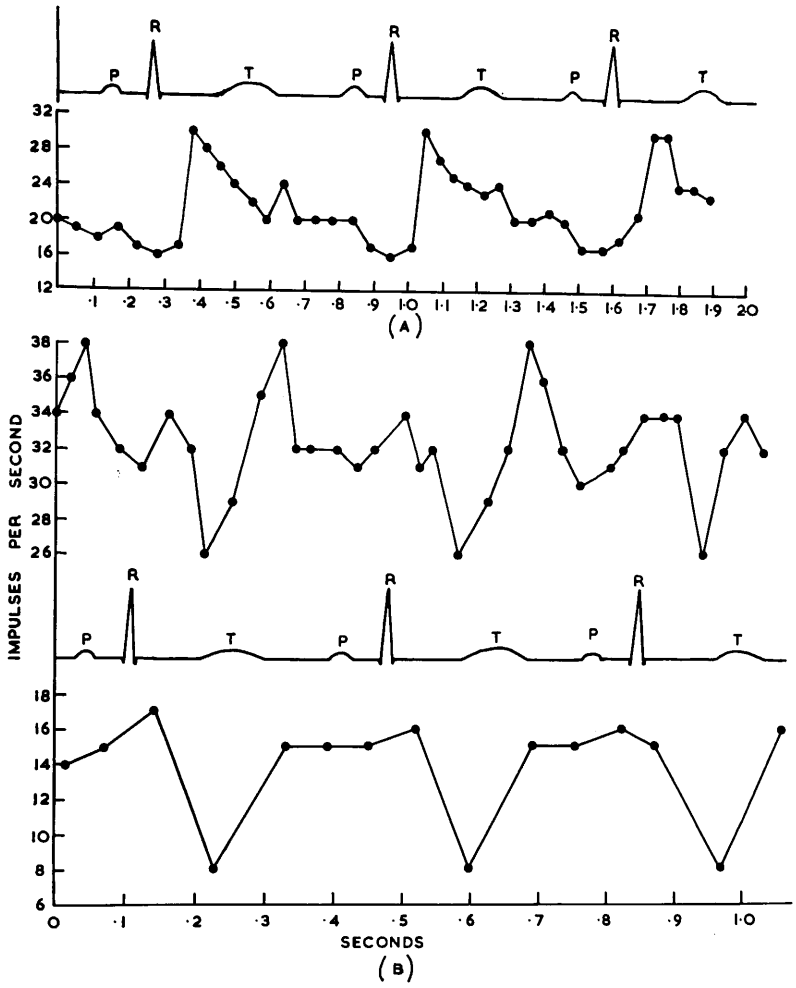



Fig. 59. Graphical representation of the responses of units affected by the pulse-beat. The corresponding electrocardiograms have been drawn diagramatically in the correct time relationship with the responses.

A) Graph of the response shown in fig. 58 B. The response during the first three cardiac cycles is plotted. (Prep. 61.)

B) Graphs of the responses shown in fig. 58 C & D; The first three cycles of each are plotted. (Prep. 84.)

which the only discharge in the position in which the record was taken was a single impulse at each pulse-wave. This type of response was recorded in fibres from both slowly and rapidly-adapting units. For the reasons given later this particular unit was classified as rapidly-adapting, though a response consisting of 'bursts' of impulses at each pulse wave was perhaps more characteristic of the rapidly-adapting type of sensory unit. In several cases a discharge from a slowly-adapting sensory unit was found to fluctuate rhythmically with the pulse-beat. Fig.58B shows such a response obtained from a unit, which had previously been discharging as in (A), but which was further stimulated by moving the joint into a new position. Figs.58C & D show the fluctuating response of a slowly-adapting sensory unit in two different positions of the joint, (D) being recorded in a position in which the unit was more stimulated than in (C). The graphs corresponding to Fig.58 B,C & D are shown in Fig.59. Fig.59A is the curve corresponding to fig.58B. In 59B are shown the two curves corresponding to fig 58C & D, plotted on the same frequency scale. The time relation of the fluctuations in frequency with respect to the e.c.g. can be seen, and where the variations take place at a higher average frequency, a second peak can be seen in the

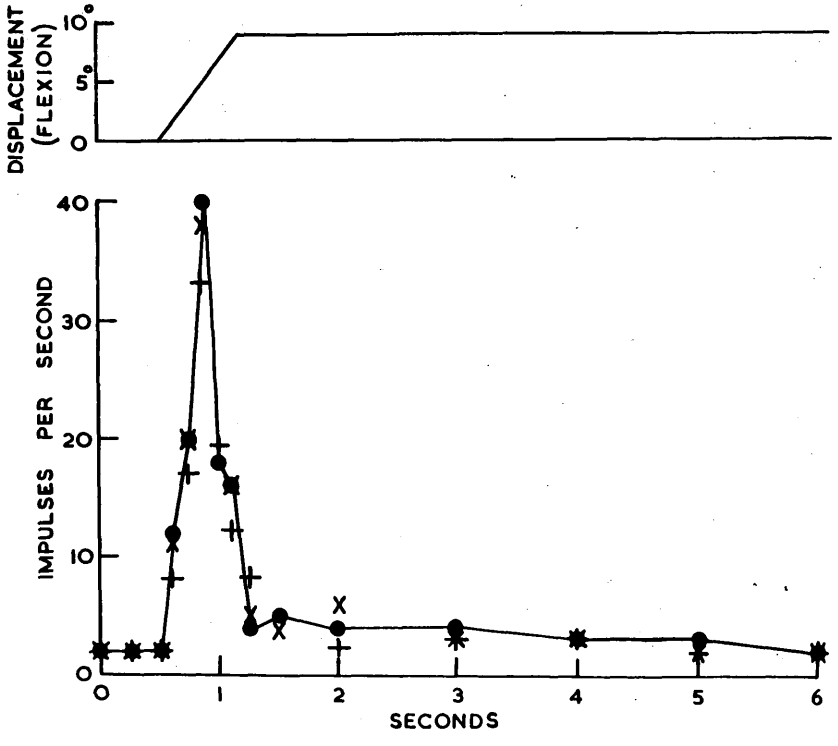



Fig. 60. Graph of the responses of the rapidly-adapting sensory unit of fig. 58 A during and after three similar movements of 10° of flexion of the joint as shown above. In each case the response is similar: the initial discharge is in time with the pulse-beat; there is increased discharge during the movement; when movement ceases the impulse-frequency rapidly falls into step with the pulse-beat again. The full line connects the values of impulse-frequency obtained during one of the movements. (Prep. 45)

response which possibly corresponds with the dicrotic wave of the pulse.

The unit of fig.58A gave rise to one impulse at each pulse wave as shown, while the joint was in a position of 128° of extension. When the joint was flexed the impulse-frequency increased considerably and then fell rapidly until it was once again in step with the pulse wave. This is shown graphically in fig.60, where the impulse-frequencies during three similar flexion movements are plotted. Although there was, in a sense, a maintained discharge it was attributed to the proximity to a blood vessel of the sensory unit responsible, and not to the position of the joint. Apart from the impulses due to the pulse wave, the unit only responded during movement and was accordingly classified as rapidly-adapting.

The response to pressure.

As has been mentioned already, most of the sensory units can be stimulated by direct pressure on the appropriate area of the joint-capsule. In a few cases, the response of a unit could not be influenced by pressure on any accessible part of the capsule, and it was assumed that these were situated in positions not accessible to the probe. The slowly-adapting units continue to

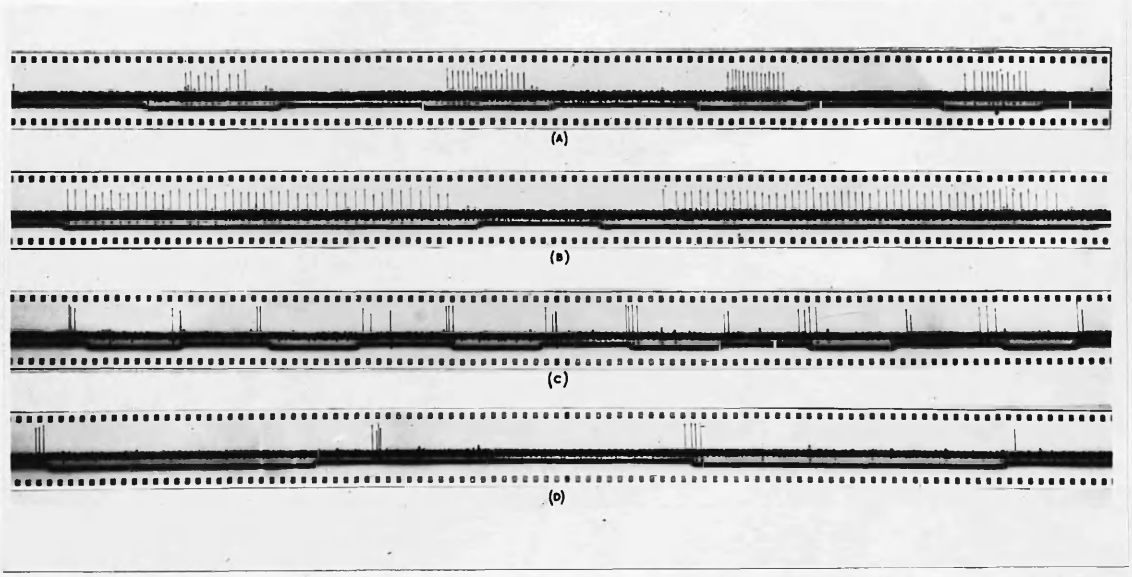



Fig. 61. Records of the response of the different types of sensory unit to direct pressure on the knee-joint capsule. The application of pressure is indicated approximately by down-step of the second beam of the oscilloscope.

A) The response of a slowly-adapting sensory unit to three short applications of pressure to the area of capsule containing the unit. (Prep.110)

B) The response of the unit of (A) to pressure maintained for a longer period.

C) The response of a rapidly-adapting unit to short applications of pressure directly over it. (Prep. 109.)

D) The response of the unit of (C) to pressure maintained for longer periods. (Prep. 109.)

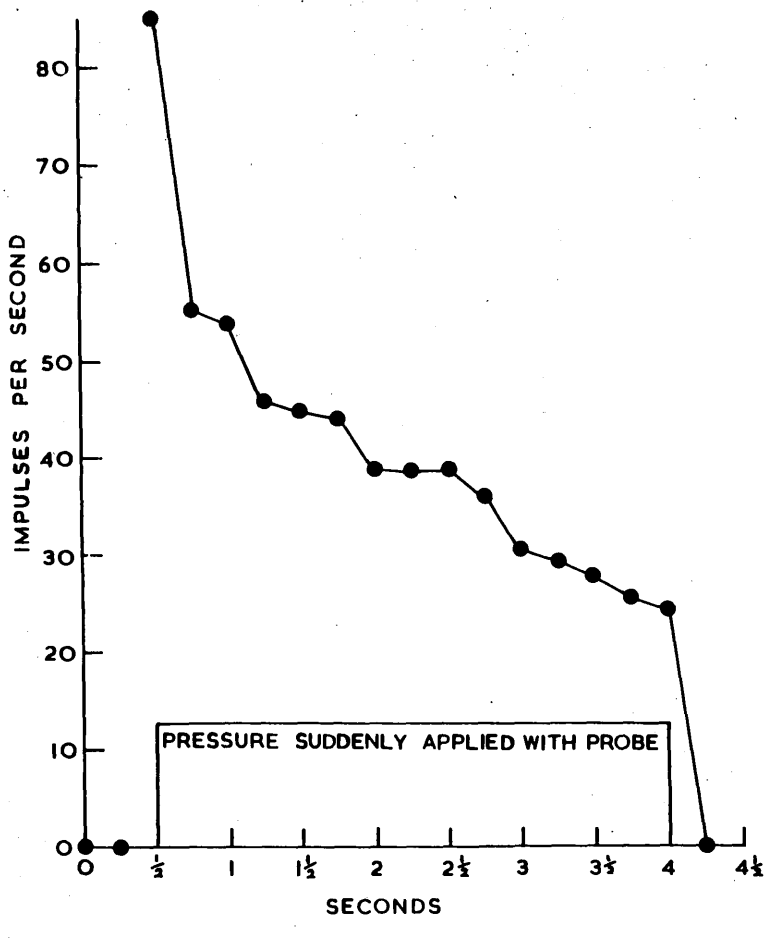



Fig. 62. Graph of the response of a single slowly-adapting sensory unit following the application of sudden pressure to the area of joint-capsule containing the unit. The pressure was maintained for the period shown by the thin line, but was released before any steady, adapted value was reached. Note that the initial frequency is higher than that usually encountered in a response to movement of the joint. (Prep. 30.)

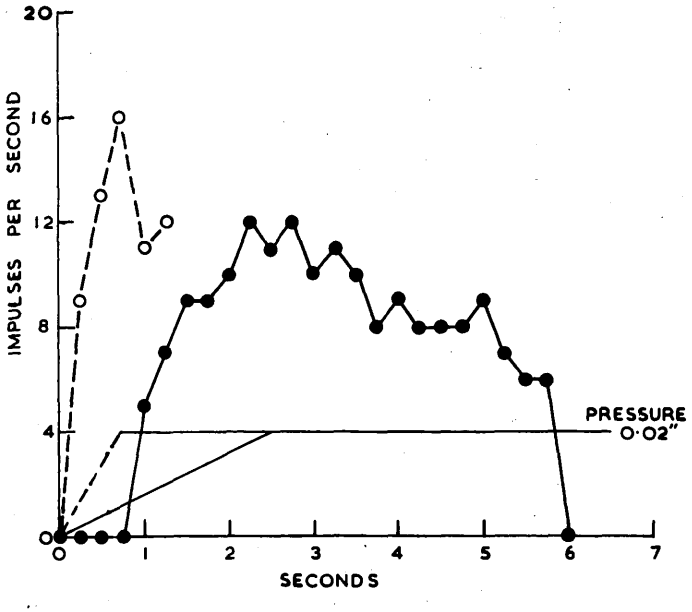



Fig. 63. Graphs of the responses of a single slowly-adapting unit to the application of direct pressure over it at two different steady rates as shown by the thin lines. The peak value is greater with more rapid application of pressure. (Prep. 41 B.)

discharge as long as the pressure is applied. This is shown in the records of fig.61A & B. Fig.61A shows the response of a slowly-adapting unit to several applications of pressure for a short period approximately indicated by the depression of the second beam of the oscilloscope. Fig.61B shows the response to pressure for a longer period - the discharge is maintained and shows slow adaptation. Fig.62 is a graph showing the adaptation of a response produced by sudden pressure on the capsule which was maintained for the period indicated. Pressure was relaxed in this case before a steady level had been reached; the peak frequency is considerably higher than that seen in any of the graphs of the responses to movement of the joint. In this case the pressure was applied by hand and was therefore not properly controlled. In a few cases, the pressure applicator described in Part 1, section 8, was employed, and the effect of applying pressure to the capsule in this way, at two different rates is shown in fig.63, the pin head travelling through the same distance in each case. As would be expected after observing the response to movement of the joint, the peak frequency is greater when the rate of application of pressure is greater, but since the system had many defects, and did not appear to yield any additional information about the behaviour of the

sensory units, it was only employed in a few cases.

The rapidly-adapting units, on the other hand, discharge only during the movements of application or of release of pressure. This is illustrated in fig.61 C & D. No maintained discharge is produced as a result of any of the applications of pressure. Here, again, the rapidly-adapting response is characterised by 'bursts' rather than a steady stream of impulses.

It was found that, with the slowly-adapting sensory units, if traction was applied to the area of capsule containing the unit a response of greater impulse-frequency than that produced by direct pressure could often be obtained. The peak-frequencies obtained in this way could be of the order of 200 impulses per sec, whereas the greatest peaks obtained on movement of the joint were rarely more than 100 impulses per sec. The frequency of the steady discharge, after the adaptation following a movement of the joint, was usually found to be between 10 and 40 impulses per sec. Discharges at less than 10 impulses per sec usually stopped after a few seconds.

The distribution of the sensory units.

Because of the response to pressure on the capsule, it was usually possible to locate the sensory unit responsible for the recorded discharge with a fair

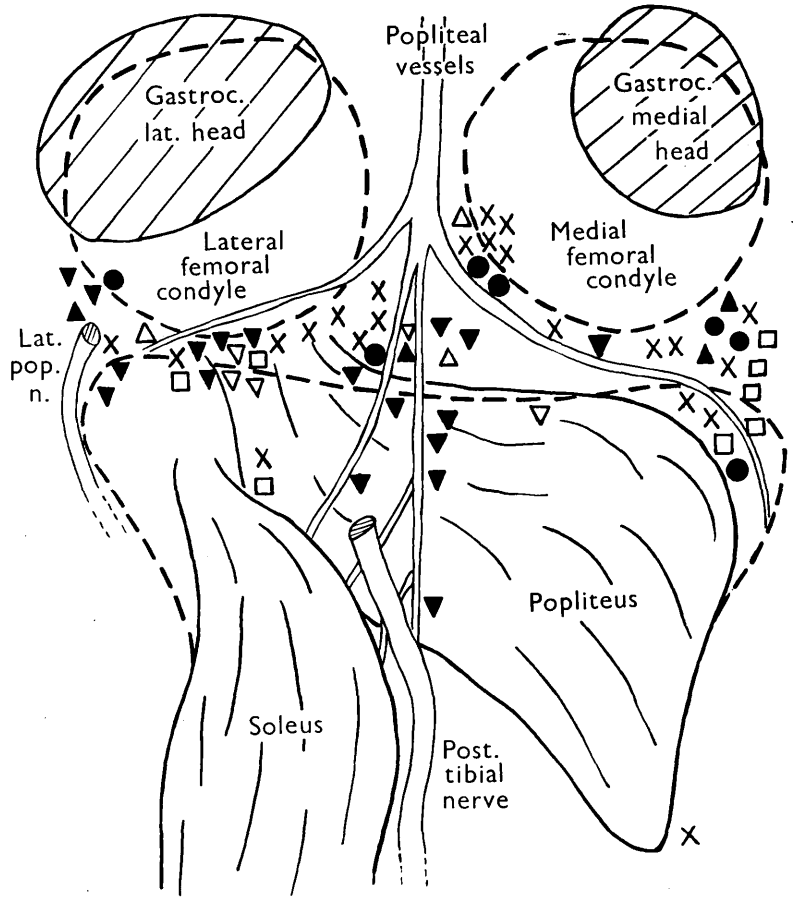



Fig. 64. Diagram of the back of the left knee-joint of the cat to show where various sensory units were located as described in the text. Slowly-adapting units are indicated according to the movements producing an increase in impulse-frequency as follows: ●, outward twisting of the tibia; ▲, outward twisting of the tibia and extension; ▼, outward twisting of the tibia and flexion; ▽, flexion; Δ, extension; X, direct pressure (movement not investigated). □ indicates a rapidly-adapting sensory unit.

degree of accuracy, by the method described in Part 1, Section 10. A number of slowly-adapting sensory units, whose behaviour was known, were localized at the positions indicated by the triangles and circles in fig.64. Discharges were also obtained from slowly-adapting units at positions indicated by the crosses when pressure was applied with a probe. It will be seen that the majority of the sensory units lie near a line across the middle of the back of the joint. There is, however, not sufficient evidence to make it possible to predict, from the position of a sensory unit in the capsule, the nature of its response to movement. Rapidly-adapting sensory units were located in the positions marked with the squares, and it will be seen that these tend to lie towards the sides of the joint rather than in the centre of the back of the capsule.

## DISCUSSION.

### (a) The slowly-adapting discharge.

The results show that the posterior articular nerve to the knee-joint of the cat carries an afferent discharge derived from sensory units of proprioceptive function. The units are capable of sustained discharge at frequencies which are dependent on the position of the joint.

A study of the adapted impulse-frequencies in various positions for a number of sensory units suggests that the steady, adapted frequency achieved by a particular unit when the joint is at rest in any position is specific for that position. This can be seen from figs. 33, 34, 36, 37, 38, 41, 42, 43, 44 in all of which the same frequency has been recorded in some position on more than one occasion, and appears to be independent of the rate of the movement used to reach that position (figs.42,43 & 44). The apparent precision is naturally dependent upon the environmental conditions of the sensory unit. Its impulse-frequency is affected, for instance, by temperature changes, and although the discharges in various positions have shown marked precision over periods of an hour or two, there is no evidence that the same specificity is maintained indefinitely, and some biological variation is to be expected.

When the position is altered, the change in frequency is exaggerated to a degree dependent on the rate of movement (figs.42, 43 & 44), and the impulse-frequency then adapts to a steady value appropriate to the new position reaching this value within about 15 secs, though sometimes further slight change persists for a minute or so. If the movement is accurately repeated, the response of the sensory unit follows the same course as before(figs.37 & 38)

For each sensory unit there is a critical position of the joint at which the discharge commences if the joint is moved through this position in the appropriate direction. The ranges over which the individual units have been found to be active show considerable overlapping and there is also much dispersion in their critical positions. This means that there is no position of rest for the joint as a whole, so far as its proprioceptors are concerned.

The sensory units responsible for these proprioceptive discharges can be localized in the posterior part of the joint-capsule overlying the line of apposition of the bones (fig.64). As several units have been found to respond by an increase in discharge on movement of the joint in more than one direction (fig.29), e.g. on flexion as well as on outward twisting of the tibia, it must be presumed that for each unit there is some direction of

deformation of the capsule which produces a maximal response. It follows that any movement resulting in a deformation with a component in this direction will produce an increase in the discharge, and it is not surprising to find that the deformations produced by the pulse-wave sometimes affect the discharge of units of this type (fig.58). Traction applied directly to the region of capsule containing a sensory unit often produces a greater frequency of discharge than can be produced by direct pressure over the unit. It is probable, then, that the sensory units are stretch-receptors responding to extension in a particular direction. If this is so, the units must be variously orientated in the capsule, and this is borne out by the localization in similar regions of the capsule of units whose responses to a particular movement are in opposite senses.

It seems likely that there may be some general relation between stimulus and impulse-frequency for this type of sensory unit. However, the relation between the position of the joint and the degree of stimulation of a particular unit must depend on the orientation of the unit as well as on the type of strain, e.g. tension or shear, imparted to the capsule. This might account for the fact that, when plotting the impulse-frequency against

position for a particular type of movement the curves obtained have different forms (e.g. fig.46). No general form for the relation between stimulus and impulse-frequency can, therefore, be deduced from the results reported here, but this does not mean that no such general relation exists.

In studying the response of a sensory unit in the capsule to a particular movement of the joint it is very important to avoid components of movement other than the one under study. The response of each unit will depend on the total amount of its deformation. Stray components of movement other than the one being studied will then have the effect of altering the apparent threshold of the unit and may also affect the slope of the stimulus-response relationship deduced in the experiment.

For a few units the curve of impulse-frequency against position in a particular range of positions has been found to shift slightly along one of the axes between one set of readings and another without, however, changing its shape (fig.46 C & D). Such a shift along the position-axis has often been observed when twisting movements were being studied. Here a slight sideways movement of the ankle between sets of readings could account for the shift of the curve, as it would have the effect of altering the

conditions of strain in the joint-capsule and would give the appearance of a change in the position taken as zero. Further, the slight changes in temperature which occur when the heaters are turned off for a time during recording could produce a shift along the frequency axis as well as a change in slope. There are, therefore, sufficient known factors to account for any observed differences in the position-frequency specificity when the position is approached from the same direction on each occasion.

It does not necessarily follow, however, that in any one position the adapted frequency of response of a particular unit will always be the same (assuming that the environmental conditions remain unaltered). Where the same frequency in any one position was observed on more than one occasion, as recorded on the graphs already referred to in this discussion, the position was always approached in the same direction. In figs. 34 & 36 movements in both directions between the two positions were employed, but each of the positions was again approached from one direction only. For example, in fig. 36 the value of 19 impulses per sec obtained in the position of 85° of extension (10° on the graph) in each cycle of movement was obtained in both cases after a

movement of flexion from 95° to 85°, and the value of 12 per sec, obtained in the position of 95° of extension (0° on the graph) at the end of each cycle, was obtained after the return movement of extension. There is no record of the value which would have been obtained if the position of 85° had been approached by a movement of extension, and that of 95° by a movement of flexion. The same argument applies to both the units whose responses are graphed in fig.34.

Figs. 47 & 48, on the other hand, show that the steady, adapted frequency in any position may depend on the direction of the movement used to reach that position. In fig.47 the position of 85° of extension was reached both by flexion and extension - the frequency after flexion was 11 impulses per sec, whereas that after extension was 9 impulses per sec. In fig.48, the position of 100° of extension was approached both by flexion and by extension - the adapted frequency after flexion was 18 impulses per sec, while that after extension was about 14 or 15 impulses per sec. It was to investigate these directional differences that the curves shown in figs. 49-56 were constructed using the pulse-interval meter. These curves have already been described, and it can be seen that the effect on the

adapted frequency of the direction used to reach a particular position varies from unit to unit. In some it is marked, the graph of a full cycle of increments of movement having a 'hysteresis' form; in some it is small, the difference being no greater than the fluctuations which occur in the steady value when the joint is maintained in any one position; and in some cases the effect is absent.

It may, therefore, be stated that the frequency in any position is independent of the rate of movement used to reach that position, but is not always independent of the direction of movement employed. The directional differences in adapted frequencies cannot be attributed to frictional forces between the connective tissue bundles in which the sensory units lie and the surrounding bundles; if this were the case the frequency of the impulses in any position reached after stretching the unit would be less than that when the same position was reached by a movement which relaxed the unit. The observed effect was the opposite of this - the frequency was greater after stretch to one position than after relaxation to the same position. The 'exaggeration' in the response to movement may be explained by supposing that the sensory unit lies in tissue less viscous than the surrounding

capsule: it would thus be subjected to greater stretch or relaxation than the surrounding tissue during a movement, but when the movement ceased the surrounding fibres would continue to change in length for a few seconds till a position of stability was reached in which the unit was less stretched than it was while the movement was taking place. If this recovery process were incomplete, the adapted frequency would be greater than if complete recovery had taken place. Similarly, during a movement which resulted in relaxation of the fibres containing the unit, this relaxation would be greater than that of the adjacent fibres (and the frequency of response lower) and then more gradual relaxation of the adjacent fibres would be accompanied by an increase in tension in the unit and the frequency would climb up to some new value. If the recovery process were incomplete, the frequency would be less than it would be if complete recovery had occurred. In any position, therefore, the frequency after adaptation would be less if the preceding movement resulted in relaxation of the sensory unit than if it resulted in stretch of the unit.

The extent of this effect might be influenced by the proportion of the strain applied to the sensory unit which

was shear rather than tension; this might account for the variation in the directional effect which is shown between one sensory unit and another. Further study of the behaviour of the sensory units is necessary before any definite conclusions may be drawn.

The sense of position.

The precision of the responses to the position and movement of the joint is very remarkable, and current concepts of the nature of joint-capsules may have to be modified. It is clear, however, that a system of sensory units responding in the manner described would be capable of providing accurate information about the position and movement of the joint. The information from many units would have to be integrated in assessing the relative position of the bones forming a joint, but such a process of integration appears to be necessary also for other senses besides position-sense.

It has sometimes been supposed that position-sense is derived from the receptors in muscles and tendons whose behaviour was described by Matthews (1933). If the position of the joint had to be deduced from information given by muscle-spindles and tendon-organs, the process of integration would be much more complicated than that required for the joint proprioceptors alone, as the

length of all the muscles at the joint would be involved. Further, the length of a particular muscle at any moment cannot be deduced by any simple process from the frequencies of the discharges from its muscle-spindles and tendon-organs, as these frequencies are affected by the tension in the muscle as well as by its length. Additional factors which might have to be taken into account include the motor discharge to the muscle, the positions of other joints, the position of the body relative to gravity, the places at which the body is supported, and the magnitude and position of any externally applied load.

The nature of the sensory units.

If the behaviour of the sensory units in the joint-capsule is compared with that of other types of unit which respond to deformation, certain general points of resemblance may be detected. Three features in particular are common to many slowly-adapting units: continued deformation leads to a sustained discharge; a change in deformation produces a change in impulse-frequency often greater than that needed to reach the steady frequency appropriate to the new conditions; where the impulse-frequency falls below about 10 impulses per sec there is a tendency for the discharge to stop altogether. These features are shown by muscle-spindles and tendon-organs

(Matthews, 1933; Cooper, Daniel & Whitteridge,1951), by receptors in the cat's toe (Adrian and Umrath,1929; Gray and Matthews 1951), by neuromast organs in the labyrinth (Lowenstein and Roberts, 1949), and by a number of other receptors.

Comparison of the slowly-adapting sensory units in the joint with the A1, A2 and B organs of Matthews (1933) shows that in range of impulse-frequency the units in the joint most closely resemble the B organs, while in the degree of exaggeration shown by the response during movement they fall into an intermediate position between the A organs and the B organs. There is also a further similarity between the A1 organs of low threshold and the sensory units in the joint in that both usually show a complete stoppage of the discharge when the degree of stimulation is reduced,the discharge picking up slowly to the new appropriate steady frequency. The classification of stretch-receptors in muscle as A organs and B organs according to their behaviour during a muscle-twitch is, of course, only an indication of the different anatomical positions of the receptors in the muscle and no such classification is applicable to the units in the joint.

The C organs described by Matthews are similar to the rapidly-adapting units in the knee-joint, both in the nature of their responses and in the comparatively small

number of the occasions on which they are encountered. It is convenient here to draw attention also to the nature of the discharges observed by Adrian and Umrath (1929) in the nerve from the cat's toe. These discharges showed slow adaptation, and were attributed to Pacinian corpuscles lying on either side of the toe beneath the tendons. The discharges were produced both by direct pressure over the groups of corpuscles and by bending the toe. Gray and Matthews (1951), in repeating these earlier experiments, observed two distinct types of discharge, a slowly-adapting one and a rapidly-adapting one consisting of impulses of larger size. They came to the conclusion that the Pacinian corpuscles were responsible for the rapidly-adapting discharges, and that the slowly-adapting discharges were derived from other, unidentified receptors. It seems probable that the slowly-adapting responses obtained by both teams of workers may have come from sensory units situated in the inter-phalangeal joints and similar in function to the units in the knee-joint described in this thesis. In addition, the rapidly-adapting discharges from the knee-joint might be derived from units similar to Pacinian corpuscles. The ratio of the two sizes of impulses observed by Gray & Matthews is the same as the ratio of the two sizes of

impulses found in the articular nerve from the knee-joint, and this fact lends further support to the view that they were dealing with a preparation comparable to the one here described.

The physiological role of the slowly-adapting sensory units.

The nerves to the knee-joint of the frog are known to develop early in embryonic life, although in the adult animal they are very small (Taylor, 1943), and there can be no doubt that the information provided by the sensory units in the joints would be extremely useful in the control of posture and in the execution of fine movements.

Gardner (1950) was unable to produce any specific reflex effects by direct stimulation of the articular nerves to the knee-joint. It is, however, clear that the influence of joint position in the control of posture must depend on the pattern of discharges in a great number of nerve-fibres so that no particular joint position would be simulated by mass stimulation of a whole nerve-trunk. This may account for Gardner's failure to produce clear-cut effects from such stimulation.

Kelton & Wright (1949), in a study of the 'easy standing' position in man, in which the hip and knee-joints are locked against ligaments and the body is supported with a minimum of muscular activity, found that

action-potentials occurred in the soleus and tibialis anticus muscles only at the limits of small swaying movements. They calculated the degree of angular displacement at the ankle-joint which just produced muscular activity during these swaying movements and found it to be very much less than that necessary to give stretch-reflexes in the same muscles in other attitudes of the limb. They concluded that the initiation of muscular activity which restores balance during swaying cannot be a simple stretch-reflex. They do not discuss the possibility that the effect may arise in the joints.

Small angular movements of the knee-joint of the cat have been shown to produce quite marked changes in impulse-frequency. Although no measurements have been made which could be compared with the threshold displacement of the human ankle-joint (reported by Kelton & Wright as $0^{\circ}\ 24'$) it is not unreasonable to suppose that sensory units in the ankle-joint may play some part in the maintenance of the easy standing position. The conclusion that a simple reflex cannot explain the facts is, however, equally applicable to reflexes arising from the joints, since the angular displacement just necessary to produce muscular activity has been found by Kelton & Wright to be dependent on the position of the limb. Some other

explanation must therefore be sought for this phenomenon.

From the finding by McCouch, Deering and Ling (1951) that the site of origin of the postural neck reflexes is restricted to the intervertebral joints, it may reasonably be presumed that these joints contain sensory units similar to those described in the knee-joint and that it is the response of these units which initiates the neck reflexes.

The cutaneous nerves to the fingers give branches to the interphalangeal joints and Stopford (1921) found, during the study of lesions due to injury, that if these nerves to the joints are destroyed, the patient can appreciate passive movement of the joints but loses the power of accurate subjective localisation of the fingers. It is known that the human knee-joint has many histological resemblances to the knee-joint of the cat (Gardner, 1948a; Samuel, 1948). It may well be, then that there are, in the human knee-joint and in other human joint-capsules, sensory units similar in behaviour to the slowly-adapting units described in this thesis. If this is so, the precision of the responses to position shown by these units would be admirably suited to the finely controlled movements on which so much human skill depends.

## PART 3.

## THE HISTOLOGICAL STRUCTURE OF THE SENSORY UNITS

## REVIEW OF LITERATURE

Histological examination of joint-capsules has been carried out by many workers, and a number of different types of receptor has been described. Hénocque (1869) described Pacinian corpuscles in the periarticular tissues, free nerve-endings within the joint, and on one occasion he found in a ligament a nerve-ending resembling a corpuscle of Meissner.

Krause (1874) described 'end-bulbs' in the synovial membrane of human interphalangeal joints, and also found Pacinian corpuscles in extracapsular tissue.

Rauber ( 1874) did not agree that these 'end-bulbs' were in the synovial membrane, but described Krause corpuscles in the fibrous capsule and extending deep into the periosteum of the human finger; he also found what he called 'modified Vater-Pacinian corpuscles' in ligaments and along the articular nerves.

Hagen-Torn(1882) found non-encapsulated endings in the fibrous capsule of the knee-joint of the cat, of the rabbit and of the dog, and simple forms of Pacinian corpuscle in the joints of the guinea-pig and rabbit.

Sfameni (1902) found abundant nerve-endings, similar to those described by Ruffini, in the periosteum, ligaments and joint-capsules of a number of different animals. He stated in his text that several of these Ruffini endings were supplied by a single axon, and, in the periosteum of the long bones of the dog, they ranged from 640μ to 1.8mm

in length, and 130μ to 700μ in breadth. The fibres supplying these endings ranged from 11μ to 22μ in diameter. He stated that he had found endings in the fibrous part of the capsule of the knee-joint of the dog which were similar to those in the periosteum in form and in size. He found neither Pacinian corpuscles nor Krause end-bulbs in the tissues he examined, but on one occasion he found two oval, encapsulated endings supplied by a single axon.

Gardner (1944) found nerve-endings which he described as 'typical Ruffini endings' in the fibrous part of the knee-joint capsule of the cat. These endings were most numerous over the posterior aspect of the joint, and 1-7 of them were supplied by the same axon. His illustrations show the Ruffini endings to be of the order of 100μ long and 50μ broad. They were supplied by nerve-fibres having diameters from 7μ to 10μ; nerve-fibres of diameters in this range form a large group of the fibres in the posterior articular nerve. He suggested that these endings might be proprioceptive in function. He also found free nerve-endings in the fibrous capsule, but stated that there were no Pacinian corpuscles in or near the joint.

Samuel (1948) stated that there were free nerve-endings, club-shaped endings, capsulated endings and Ruffini-like endings in the fibrous capsule of the knee-joint of the cat. The Ruffini-like endings occurred 'infreguently in normal tissue'.

It is obvious that there is considerable variation in the findings of these different workers, and the endings described do not fall naturally into any two categories which might be correlated with

the slowly-adapting and rapidly-adapting discharges already described. It was therefore decided to make a further histological examination of the knee-joint capsule of the cat, using the Gold Chloride technique of Gairns (1930), which is particularly suitable for the demonstration of nerve-endings. Details of the histological technique have already been given in Part 1, section 11. The results of this investigation will now be described.

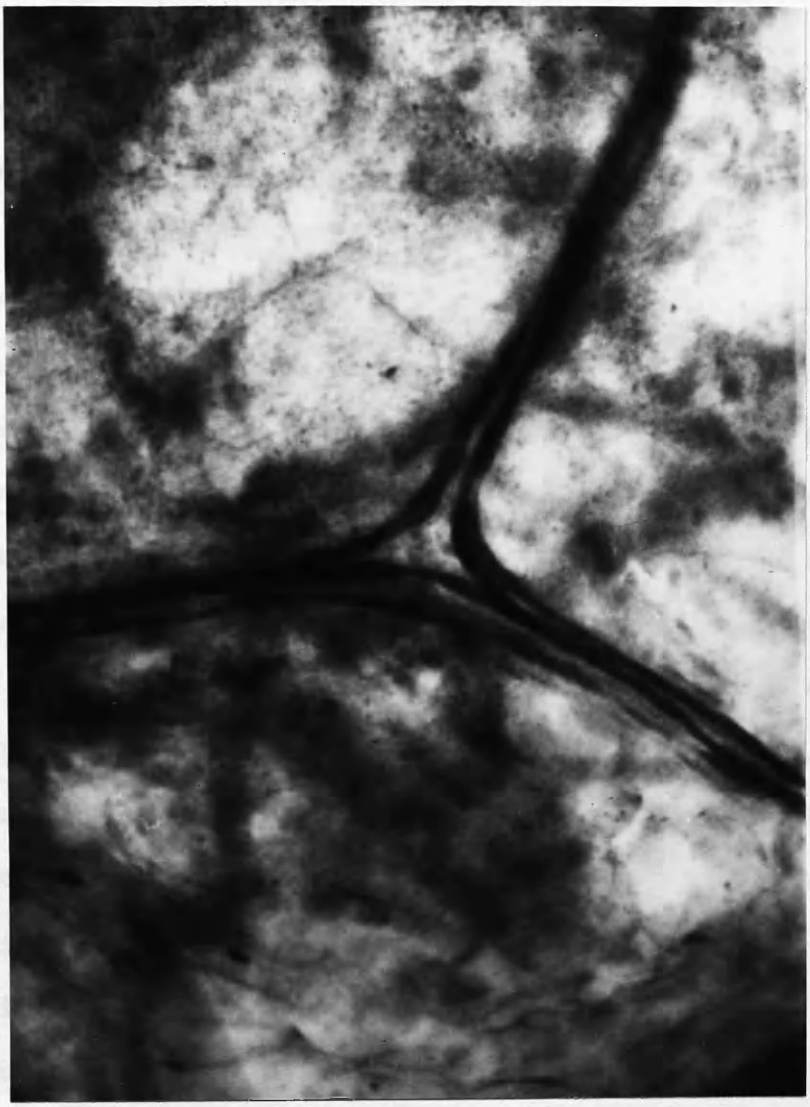




Fig. 65. An example of the curious type of nerve distribution to be found in the joint-capsule. Nerve-fibres approach and separate again in such a way that it is impossible to tell which is the central, and which the peripheral, end of each fibre.

## RESULTS

### General Findings

Histological examination of tissue from 12 decerebrate cats was carried out; in 6 of these both knee-joints were employed, so that receptors in tissue from 18 different knee-joints were studied. In a few cases the whole of the posterior capsule was stained and examined; in other cases smaller portions of capsule were taken from selected areas so that the distribution of the receptors could be assessed; the histological findings of the examination of the small pieces of capsule removed in the experiments described in Part 4 have also been included in the results now described. Tissue from the popliteus muscle and tendon, and from the sides of the joint, was also examined.

Most portions of capsule are richly supplied with nerves. Many of these accompany blood vessels, forming a network around and alongside of them. Other axons spread throughout the fibrous layer of the capsule, dividing and joining one another so that it is often impossible to tell which is the central end of each fibre. It is common for two or more fibres lying close together to diverge and each to join company with other fibres or groups of fibres. An example of this curious type of nerve distribution is shown in fig. 65, where three fibres come into relation with each other in such a way that it is impossible to tell which is the central or peripheral portion of each one. In relation to the number of branching nerve-fibres, the number of receptors encountered was relatively small. Some fibres were

| No. of sprays to one unit | No. of sensory units with the indicated no. of sprays |
|---|---|
| 1 | 6 |
| 2 | 7 |
| 3 | 13 |
| 4 | 8 |
| 5 | 14 |
| 6 | 4 |
| 7 | 4 |
| No. unknown | 18 |
| Total | 74 |

Fig. 66. Table showing the number of spray receptors of which 74 spray sensory units were composed. In some cases a sensory unit was situated in fibrous tissue so densely stained that it was not possible to be certain that all the receptors comprising it had been counted. Such units have been classified in the table as consisting of an unknown number of sprays.

traced for long distances from the point of departure from a parent trunk before receptors were found.

Within the fibrous layer of the knee-joint capsule two definite and quite distinct types of sensory unit have been found, a 'spray' type and a 'lamellated' type. No organised nerve-endings were found elsewhere in the capsule. On a few occasions the staining was such that a receptor could not be clearly classified into either of these types, and in a further group of cases nerves were found to terminate in what may or may not have been true receptors. On one occasion part of one of the cruciate ligaments was examined and found to contain typical tendon organs of Golgi. Tissue from the popliteus muscle and its tendon was found to contain muscle-spindles and tendon-organs.

The 'spray' type of sensory unit.

Sensory units of the spray type are by far the most numerous. They are distributed throughout the capsule but are present in greatest number in the centre of the back of the joint. Each sensory unit consists of from 1 to 7 sprays supplied by a single axon, those consisting of 5 or less being the most common. Fig. 66 is a table showing the number of sprays of which 74 sensory units were composed. A considerable number of the sensory units examined were embedded in densely impregnated fibrous tissue, and while there was no doubt about the type of unit present, it was not possible to count all the individual receptors of which it was composed. These sensory units have been recorded in the table as consisting of an unknown number of sprays.

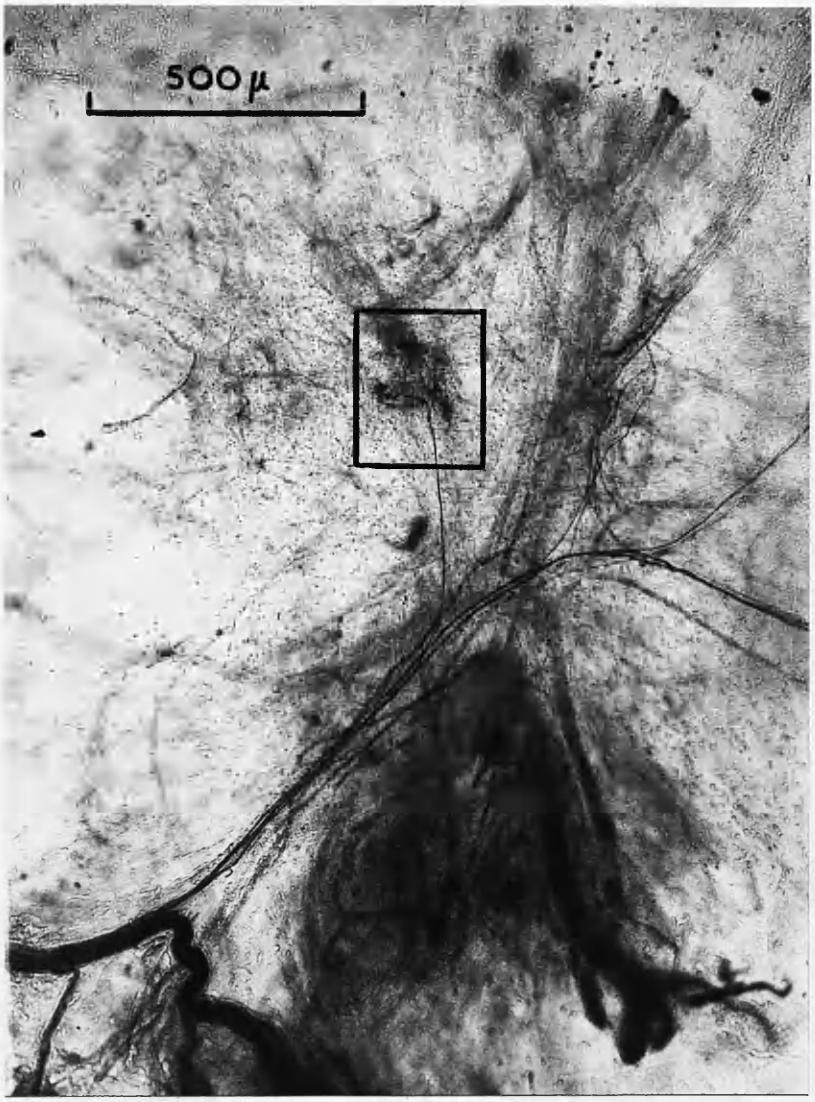



Fig. 67. A nerve trunk, in the fibrous layer of the capsule of the knee-joint of the cat, giving rise to a single axon which ends in a sensory unit of the spray type. (Gold chloride.)


Fig. 68. The sensory unit outlined in fig. 67 at greater magnification. Note the three sprays arising from branches of a single axon. (Gold chloride.)

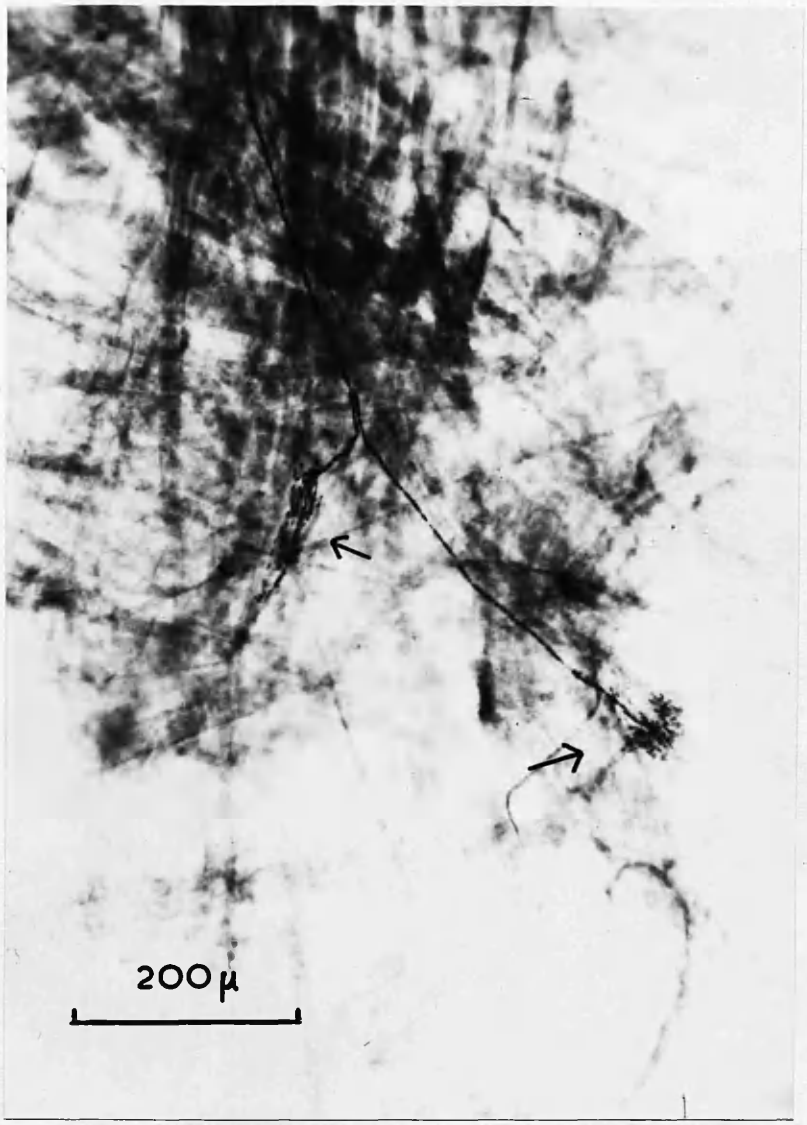



Fig. 69. A sensory unit of spray type in the fibrous layer of the joint-capsule. The unit consists of two sprays, indicated by the arrows, supplied by branches from a single axon. (Gold chloride)

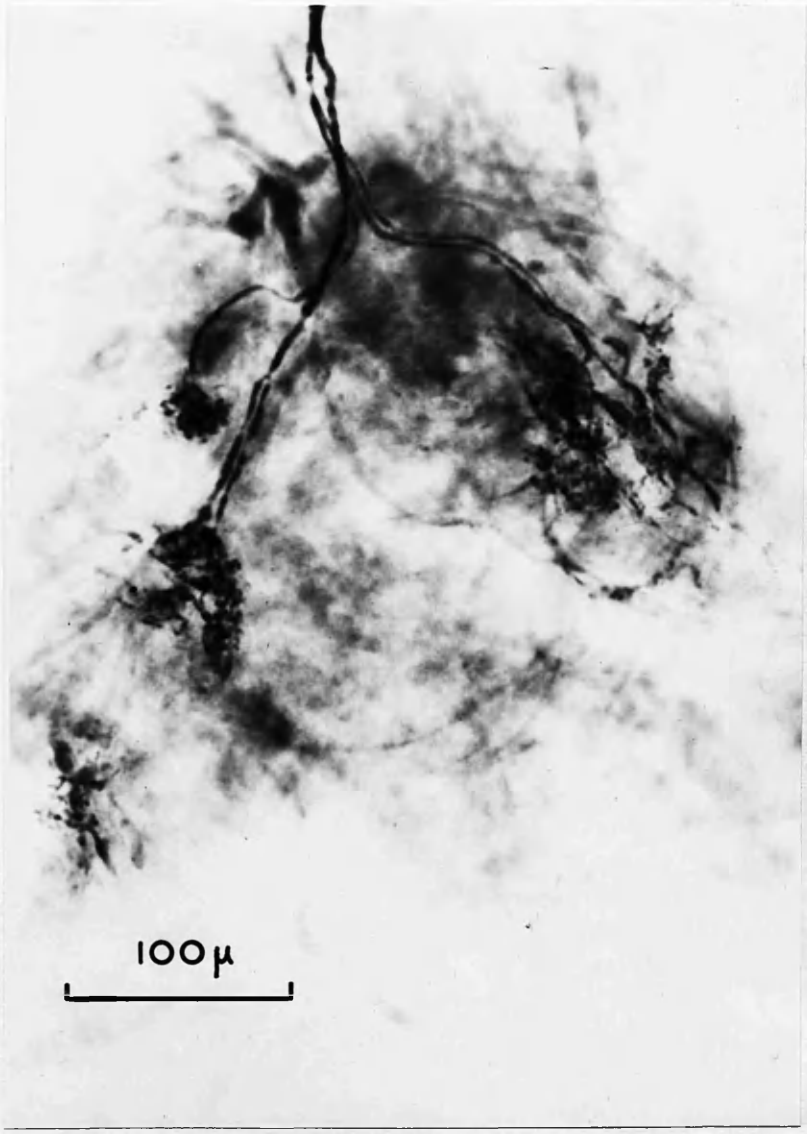



Fig. 70. A sensory unit in the fibrous capsule, consisting of a number of sprays. (Gold chloride)

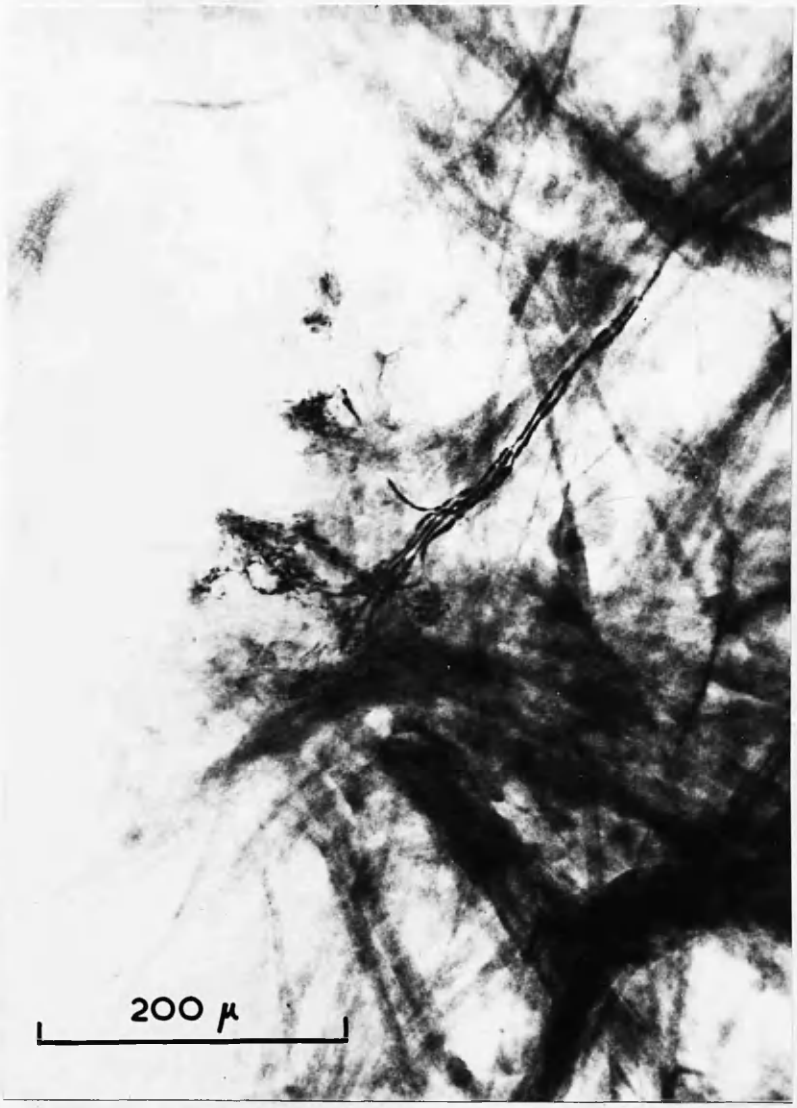



Fig. 71. A sensory unit in the fibrous capsule, consisting of a considerable number of sprays, many of which are partially obscured by fibrous tissue. All the sprays are derived from a single axon. (Gold chloride)

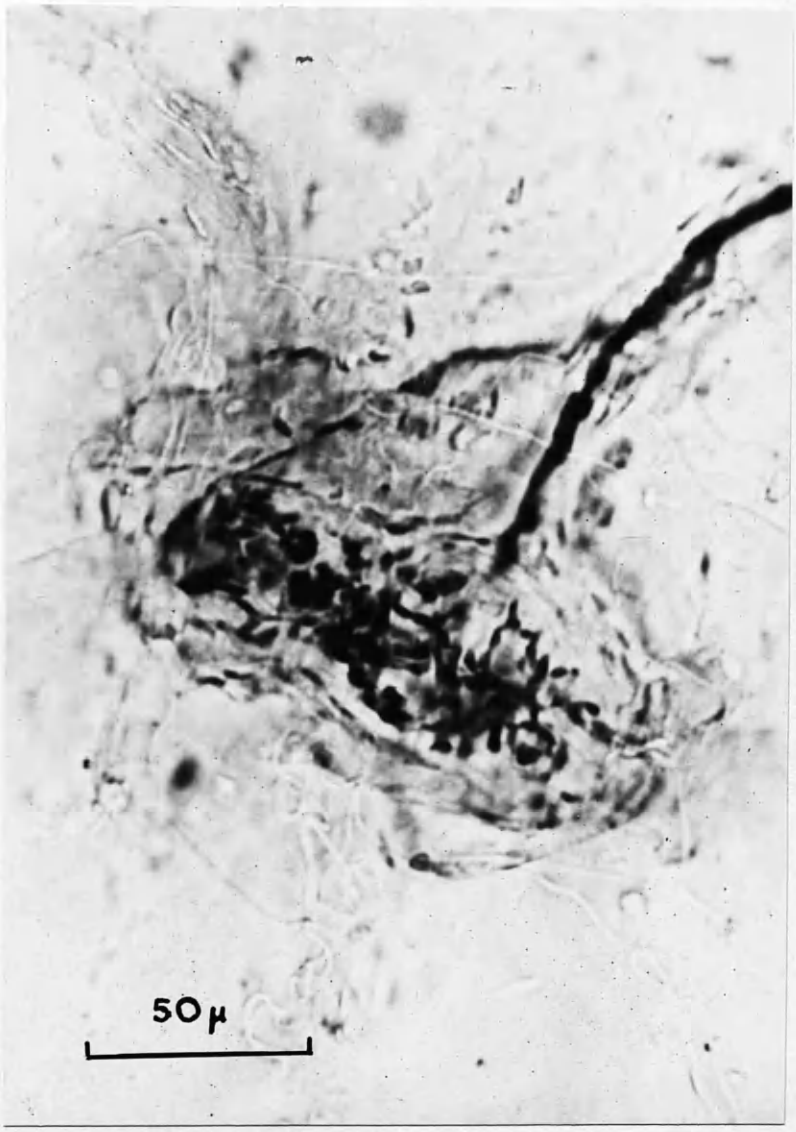



Fig. 72. A single receptor of the spray type, from the fibrous capsule, at high magnification. The spray is surrounded by several layers of cells forming a capsule. (Gold chloride)


Fig. 73. A photodiagram of one of the sprays of the sensory unit shown in Fig. 68; the detailed structure of the spray can be clearly seen. The parts of the spray not in focus in the plane of fig. 68 have been superimposed on the original photograph.

| Spray no. | Max. long. diam. (μ) | Max. trans. diam. (μ) |
|---|---|---|
| 1 | 88 | 40 |
| 2 | 140 | 24 |
| 3 | 100 | 24 |
| 4 | 80 | 28 |
| 5 | 160 | 40 |
| 6 | 80 | 20 |
| 7 | 80 | 24 |
| 8 | 72 | 28 |
| 9 | 52 | 24 |
| 10 | 52 | 24 |
| 11 | 52 | 40 |
| 12 | 92 | 24 |
| 13 | 100 | 24 |
| 14 | 200 | 16 |
| 15 | 80 | 32 |
| 16 | 52 | 40 |
| 17 | 144 | 20 |
| 18 | 140 | 20 |
| 19 | 100 | 24 |
| 20 | 120 | 24 |
| 21 | 120 | 40 |
| 22 | 100 | 32 |
| 23 | 140 | 40 |
| 24 | 80 | 56 |
| 25 | 120 | 28 |
| 26 | 52 | 32 |
| 27 | 80 | 52 |
| 28 | 60 | 28 |
| 29 | 44 | 40 |
| 30 | 100 | 28 |
| 31 | 72 | 40 |
| 32 | 60 | 20 |
| 33 | 100 | 48 |
| 34 | 60 | 36 |
| 35 | 120 | 40 |
| 36 | 60 | 40 |
| 37 | 120 | 32 |
| 38 | 80 | 28 |
| 39 | 120 | 60 |
| 40 | 100 | 40 |

| | Mean | Standard error | Standard deviation |
|---|---|---|---|
| Long. diam. (μ) | 93.8 | ± 5.5 | ± 35.1 |
| Trans. diam. (μ) | 32.8 | ± 1.6 | ± 10.2 |

Fig. 74. The dimensions of a random selection of 40 individual spray receptors.

Fig. 67 shows a nerve-trunk giving rise to a single fibre which ends in a sensory unit with three sprays. Each spray is similar in appearance to the nerve-endings described by Ruffini, consisting of small, densely-staining, particles connected together by fine, branching nerve-fibrils. Fig. 68 shows the sensory unit of Fig. 67 at greater magnification. Further examples of this type of sensory unit are shown in fig. 69, in which the unit consists of two sprays, fig. 70 in which the unit has at least five sprays, and fig. 71 in which it consists of about 7 sprays. A very thin capsule of one or two layers of cells is occasionally seen to surround the whole of each spray, and it is probable that this capsule is always present although rarely visible with the staining technique employed. Fig. 72 shows a single spray at high magnification, and the surrounding layers of capsule are clearly visible. Fig. 73 is a photodiagram of one of the sprays of the sensory unit shown in fig. 68; the portions of this spray not in the plane of focus of fig. 68 have been added to the photograph so that the detailed structure of the spray can be more clearly seen. An additional portion of spray is visible here, arising from the same axon as the first one, close to its termination; this second spray is probably part of the first one, and has become partially separated from it.

The dimensions of a random selection of 40 different sprays are given in fig. 74. They range in length from 44μ to 200μ and in breadth from 16μ to 60μ. The mean dimensions and standard error are given.

| Spray no. | Fibre diam. (μ) | Spray no. | Fibre diam. (μ) |
|---|---|---|---|
| 1 | 4 | 21 | 4 |
| 2 | 3 | 22 | 4 |
| 3 | 3 | 23 | 4 |
| 4 | 3 | 24 | 3 |
| 5 | 3 | 25 | 4 |
| 6 | 4 | 26 | 4 |
| 7 | 4 | 27 | 3 |
| 8 | 3 | 28 | 4 |
| 9 | 3 | 29 | 4 |
| 10 | 5 | 30 | 3 |
| 11 | 3 | 31 | 3 |
| 12 | 4 | 32 | 4 |
| 13 | 5 | 33 | 4 |
| 14 | 6 | 34 | 3 |
| 15 | 6 | 35 | 4 |
| 16 | 4 | 36 | 4 |
| 17 | 4 | 37 | 4 |
| 18 | 4 | 38 | 4 |
| 19 | 4 | 39 | 4 |
| 20 | 4 | 40 | 4 |

| | Mean | Standard error | Standard deviation |
|---|---|---|---|
| Fibre diameter (μ) | 3.9 | ± 0.1 | ± 0.7 |

Fig. 75. Table of the diameters of the afferent fibres from a random selection of 40 individual spray receptors.

| Unit no. | Fibre diam. (μ) | Unit no. | Fibre diam. (μ) |
|---|---|---|---|
| 1 | 6 | 19 | 8 |
| 2 | 6 | 20 | 8 |
| 3 | 5 | 21 | 6 |
| 4 | 5 | 22 | 8 |
| 5 | 6 | 23 | 8 |
| 6 | 8 | 24 | 4 |
| 7 | 6 | 25 | 4 |
| 8 | 8 | 26 | 5 |
| 9 | 6 | 27 | 5 |
| 10 | 8 | 28 | 5 |
| 11 | 5 | 29 | 4 |
| 12 | 4 | 30 | 6 |
| 13 | 8 | 31 | 6 |
| 14 | 10 | 32 | 6 |
| 15 | 10 | 33 | 7 |
| 16 | 8 | 34 | 8 |
| 17 | 4 | 35 | 5 |
| 18 | 6 | | |

| | Mean | Standard error | Standard deviation |
|---|---|---|---|
| Fibre diameter (μ) | 6.3 | ± 0.3 | ± 1.7 |

Fig. 76. Table of the diameters of the afferent fibres from a random selection of 35 spray sensory units.

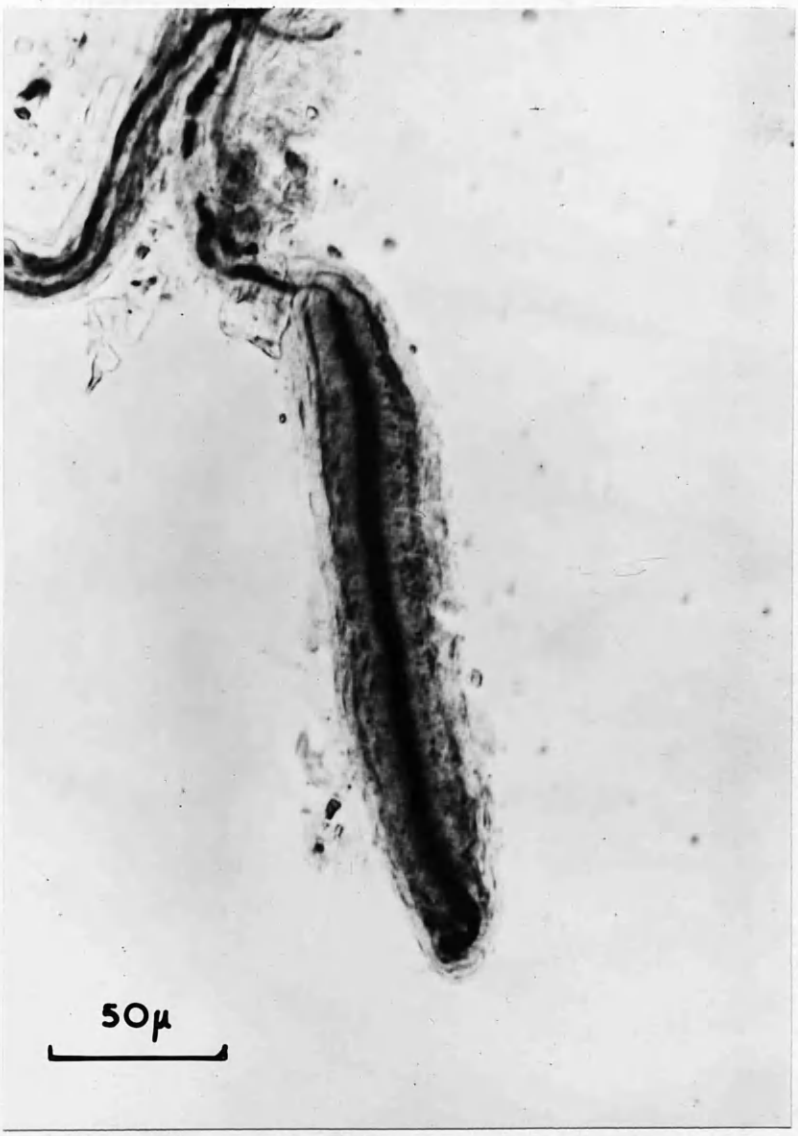



Fig. 77. A lamellated receptor isolated from the fibrous capsule. Note the central portion with its curved, knob-like, termination, the surrounding finely granular layer, and the layers of cells ensheathing the whole receptor. (Gold chloride)

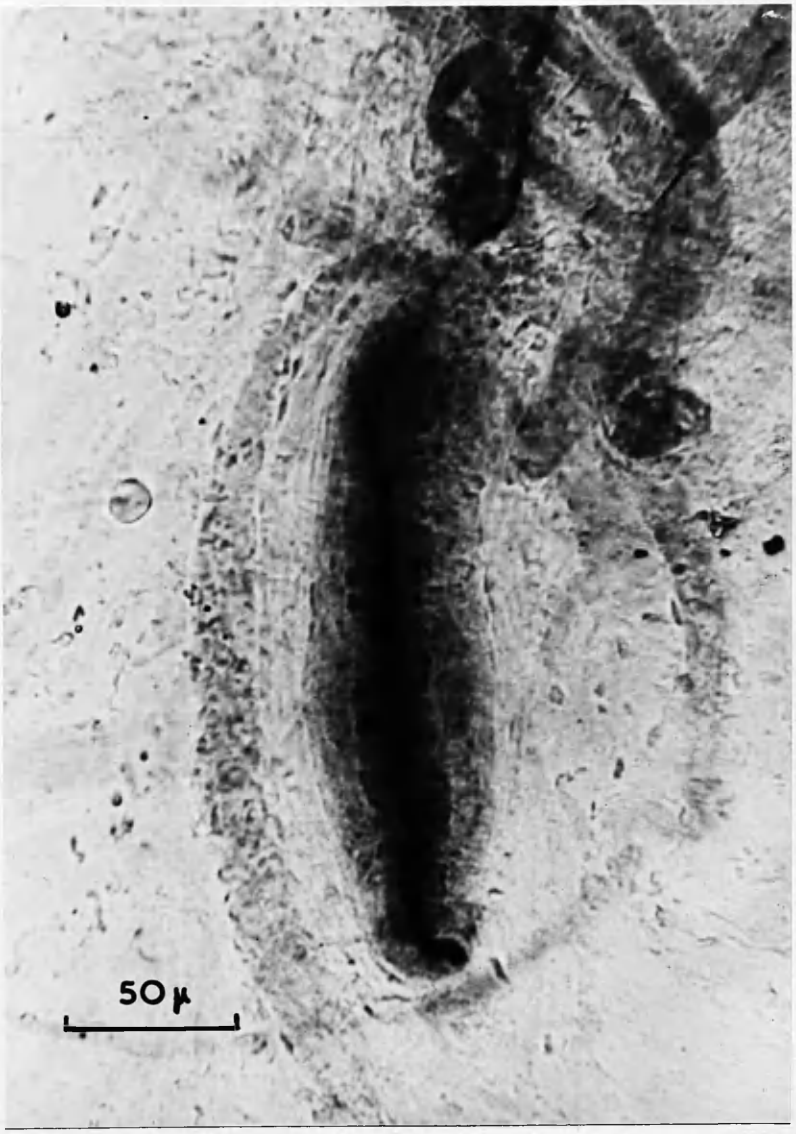



Fig. 78. A lamellated receptor from the fibrous capsule, showing the same features as does the receptor in fig. 77. Note the apparent thinning of the axon as it enters the receptor. (Gold chloride)

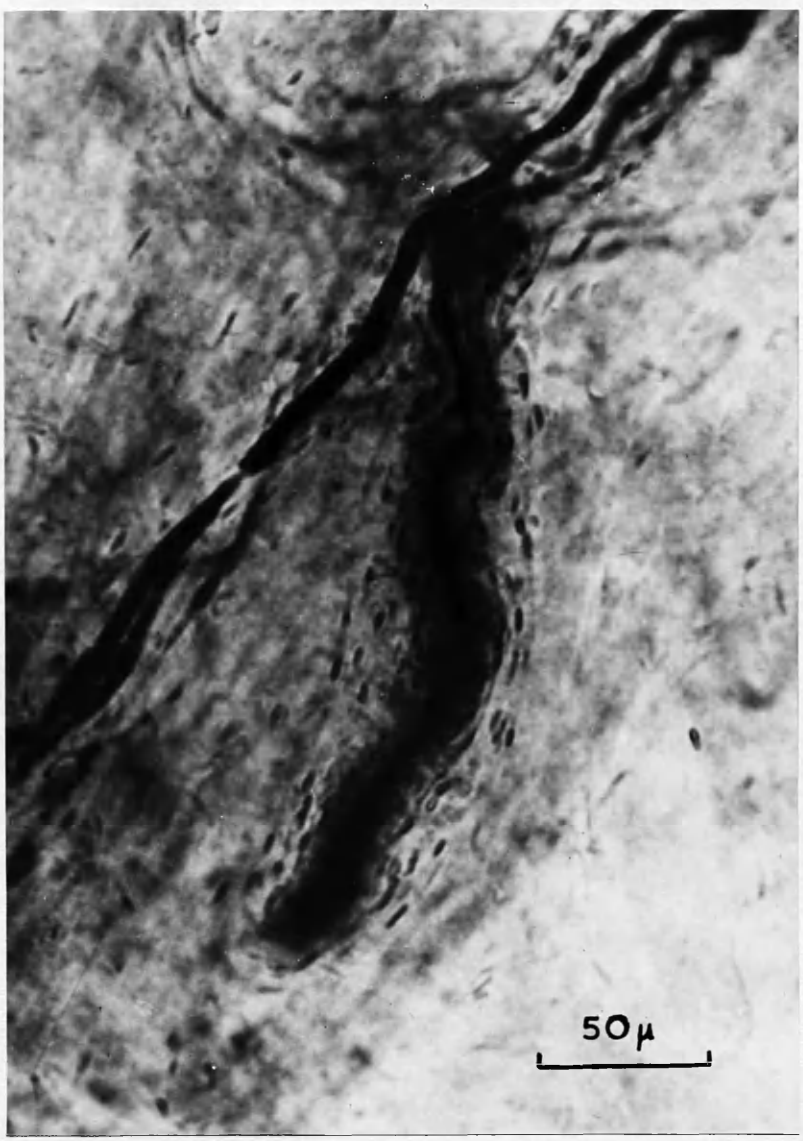



Fig. 79. A lamellated receptor from the fibrous capsule. The nuclei of the layers of cells forming the capsule round the receptor can be clearly seen. (Gold chloride)


Fig. 80. A lamellated receptor from the fibrous capsule. The central portion and the surrounding homogeneous layer can be seen but the layers of capsule are not visible. (Gold chloride)


Fig. 81. A lamellated receptor from the fibrous capsule. The nuclei of the layers of capsule round the receptor are easily seen. The central portion pursues a rather zig-zag course through the receptor; this may be an artefact due to the staining process, there being contraction of the tissue in which the receptor lies. (Gold chloride)

Fig. 75 is a table showing the diameters of the axons to 40 individual sprays; the mean and standard error is also given. Fig. 76 is a table of the diameters of the axons supplying 35 sensory units.

The 'lamellated' type of sensory unit.

The sensory units of lamellated type are much less frequently encountered, and tend to lie towards the sides of the joint rather than in the centre of the back of the capsule. These units consist of one, or of two, or, very occasionally of three elongated, cylindrical receptors supplied by branches from a single axon. Each of these receptors consists of a densely-stained extension of the axon which may run straight through the body longitudinally, or may pursue a zig-zag course through it, and which frequently ends in a knob-like expansion. Surrounding this central portion is an evenly distributed, finely granular layer, outside which is a very distinct capsule consisting of a number of concentric lamellae. This capsule is nearly always clearly visible in gold-stained preparations. Examples of this type of receptor are shown in figs. 77 - 82. In figs. 77 & 78 the densely-stained central portion, with its knob-like termination, is especially clear; the nuclei of the cells forming the layers of capsule are easily seen in fig. 79; although the layers of capsule are not distinct in fig. 80, the homogeneous layer has a clearcut outside border. The receptor in fig. 81 has a core which pursues a zig-zag course; this may, of course, be an artefact due to contraction of the tissue during the staining process. On one occasion a lamellated receptor was found to have a second,

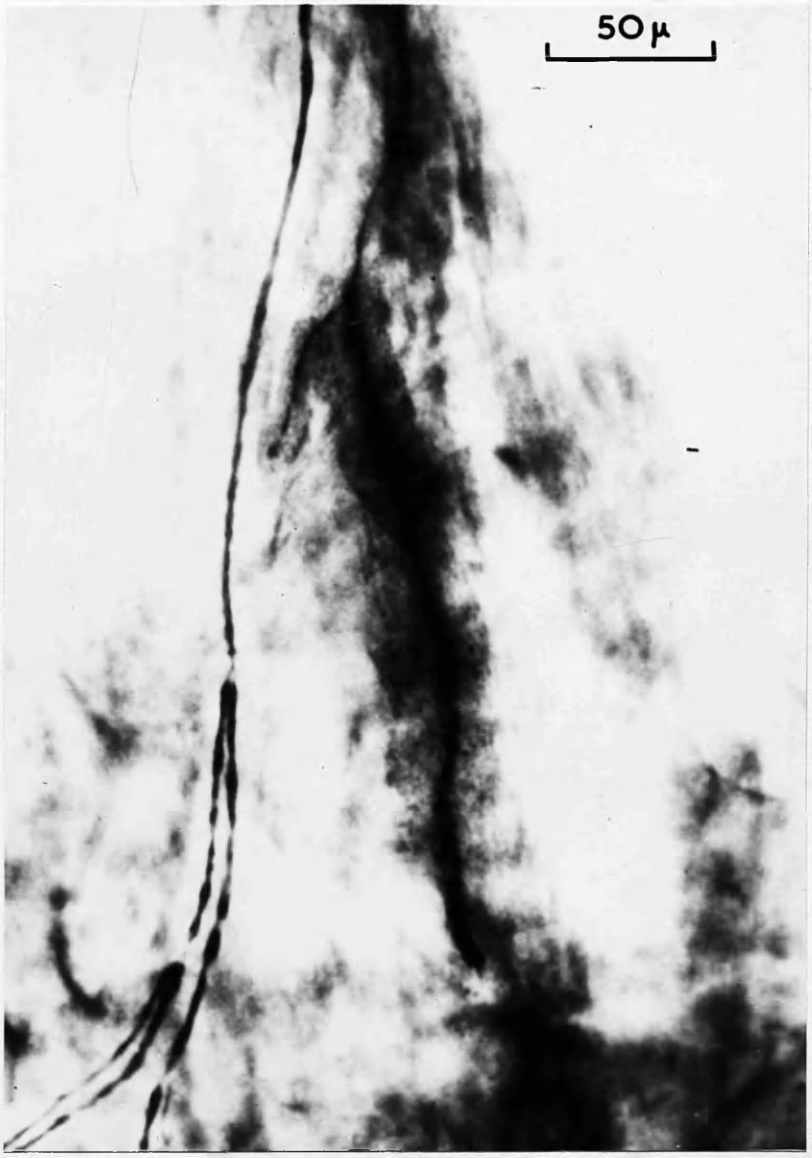



Fig. 82. A lamellated receptor from the fibrous capsule; a small bud (indicated by the arrow), of similar appearance to the receptor, can be seen attached to its base. (Gold chloride)

| No. of lamellated receptors to one unit. | No. of sensory units having the indicated number of receptors. |
|---|---|
| 1 | 7 |
| 2 | 4 |
| 3 | 1 |
| Total | 12 |

Fig. 83. Table showing the number of lamellated receptors of which 12 sensory units of the lamellated type were composed.

| Lamellated receptor no. | Max. long. diam. (μ) | Max. trans. diam. (μ) |
|---|---|---|
| 1 | 240 | 28 |
| 2 | 200 | 24 |
| 3 | 220 | 28 |
| 4 | 160 | 28 |
| 5 | 180 | 24 |
| 6 | 200 | 48 |
| 7 | 80 | 32 |
| 8 | 148 | 28 |
| 9 | 240 | 32 |
| 10 | 260 | 40 |
| 11 | 260 | 40 |
| 12 | 240 | 32 |
| 13 | 360 | 40 |
| 14 | 140 | 24 |
| 15 | 200 | 32 |
| 16 | 180 | 20 |
| 17 | 200 | 48 |
| 18 | 220 | 40 |

| | Mean | Standard error | Standard deviation |
|---|---|---|---|
| Long. diam. (μ) | 207.2 | ± 14.1 | ± 59.1 |
| Trans. diam. (μ) | 33.1 | ± 2.0 | ± 8.4 |

Fig. 84. The dimensions of 18 individual lamellated receptors.

| Lamellated receptor no. | Fibre diam. (μ) |
|---|---|
| 1 | 4 |
| 2 | 3 |
| 3 | 6 |
| 4 | 4 |
| 5 | 3 |
| 6 | 5 |
| 7 | 3 |
| 8 | 6 |
| 9 | 4 |
| 10 | 4 |
| 11 | 4 |
| 12 | 4 |
| 13 | 4 |
| 14 | 4 |
| 15 | 5 |
| 16 | 4 |
| 17 | 4 |
| 18 | 4 |

| | Mean | Standard error | Standard deviation |
|---|---|---|---|
| Fibre diameter (μ) | 4.3 | ± 0.2 | ± 0.8 |

Fig. 85. Table of the diameters of the afferent fibres from 18 individual lamellated receptors.

| Lamellated unit no. | Fibre diam. (μ) |
|---|---|
| 1 | 8 |
| 2 | 6 |
| 3 | 6 |
| 4 | 4 |
| 5 | 8 |
| 6 | 6 |
| 7 | 9 |
| 8 | 6 |
| 9 | 5 |
| 10 | 5 |

| | Mean | Standard error | Standard deviation |
|---|---|---|---|
| Fibre diameter (μ) | 6.4 | ± 0.5 | ± 1.5 |

Fig. 86. Table of the diameters of the afferent fibres from 10 sensory units of the lamellated type.

miniature, one growing out from its base (fig. 82).

The number of lamellated receptors making up each sensory unit is tabulated in fig. 83. In the majority of cases the unit consists of a single lamellated receptor, and the distinction between a sensory unit and a receptor disappears.

The dimensions of the lamellated receptors are given in fig. 84. In a sample of 18 receptors, the length ranged from 80μ to 360μ and the breadth from 20μ to 48μ. The values of the mean and standard error are given in the table. The sizes of the fibres supplying individual receptors are given in fig. 85, and the sizes of fibres to sensory units in fig. 86; there is some overlap between the readings in these two tables since in a number of cases the fibre to the sensory unit was also the fibre to an individual receptor (the unit consisting of this receptor only). Seen in three dimensions under the dissecting microscope these lamellated receptors are distinctly cylindrical in shape with rounded ends, and have a definite longitudinal core.

In the areas of capsule where both types of sensory unit are present the axon supplying the lamellated type of unit usually accompanies another axon supplying a unit of the spray type, the respective receptors lying close together. This often gives the impression that a receptor of spray type and one of lamellated type arise from the same axon. Careful examination and separation of the individual fibres under the dissecting microscope has <u>never</u> confirmed this impression. The fibres sometimes cross, and often appear


Fig. 87. A sensory unit of spray type and one of lamellated type lying in the same area of capsular tissue. The spray unit consists of a number of sprays (marked S) derived from one axon; the lamellated unit consists of one lamellated receptor (marked L) supplied by a different axon. The lamellated receptor is the one shown in fig. 82. At first sight it might be thought that receptors of the two types are supplied by the same axon; this was, in fact, not the case. (Gold chloride)

| | Tendon-organ number | |
|---|---|---|
| | 1 | 2 |
| Max. long. diam. | 500 μ | damaged |
| Max. trans. diam. | 125 μ | damaged |
| Fibre diam. | 12 μ | 12 μ |

Fig. 88. Table of the dimensions of one of the two tendon-organs found in a cruciate ligament and the diameters of the afferent fibres from both of them.

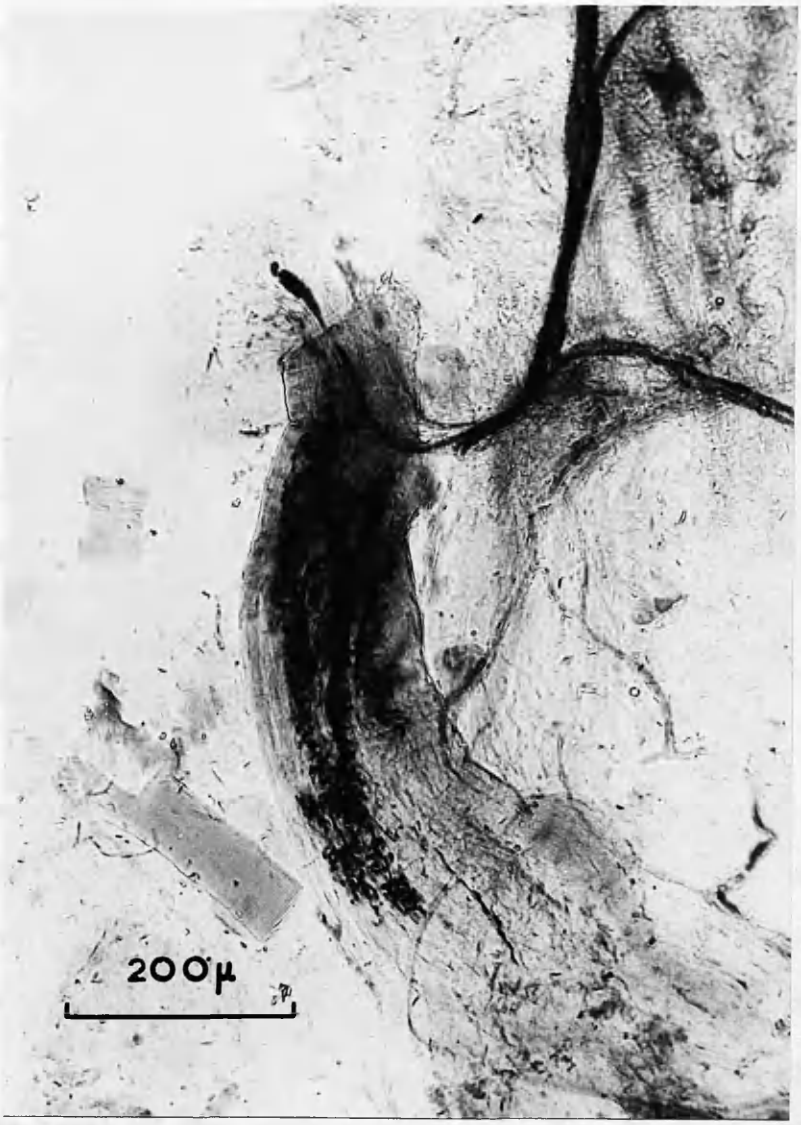



Fig. 89. A Golgi tendon-organ from one of the cruciate ligaments of the knee-joint. Note that it is much larger than the spray sensory units in the joint-capsule; the magnification is the same as in fig. 69. (Gold chloride)

superimposed along part of their course, but on no occasion on which a fibre has been seen to divide at a node, have the individual branches been found to serve receptors of different types. In fig. 87 receptors of the two types can be seen; their afferent fibres lay close together in part of their course but they did not join to form a single axon although traced for some distance through the capsule.

Other nerve-endings in the capsule.

Some nerve-fibres in the fibrous capsule are found to terminate either abruptly or to taper away gradually, no organised endings being present. Whether or not these are true nerve-endings will be discussed later.

Sensory units in cruciate ligaments

Part of one of the cruciate ligaments was examined on one occasion. Two typical tendon-organs of Golgi were found in the surface layers of the ligament. Of these only one was intact and its dimensions, and the diameters of the afferent fibres to both of them, are given in fig. 88. The intact tendon-organ is shown in fig. 89; note that it is much larger than any of the sensory units in the fibrous layer of the joint-capsule (cf. fig. 69 where the magnification is the same).

Sensory units in the popliteus muscle and tendon.

Because of its relation to the joint-capsule, it was inevitable that part of the popliteus tendon (where it passes through the capsule), and the muscle close to its insertion, were

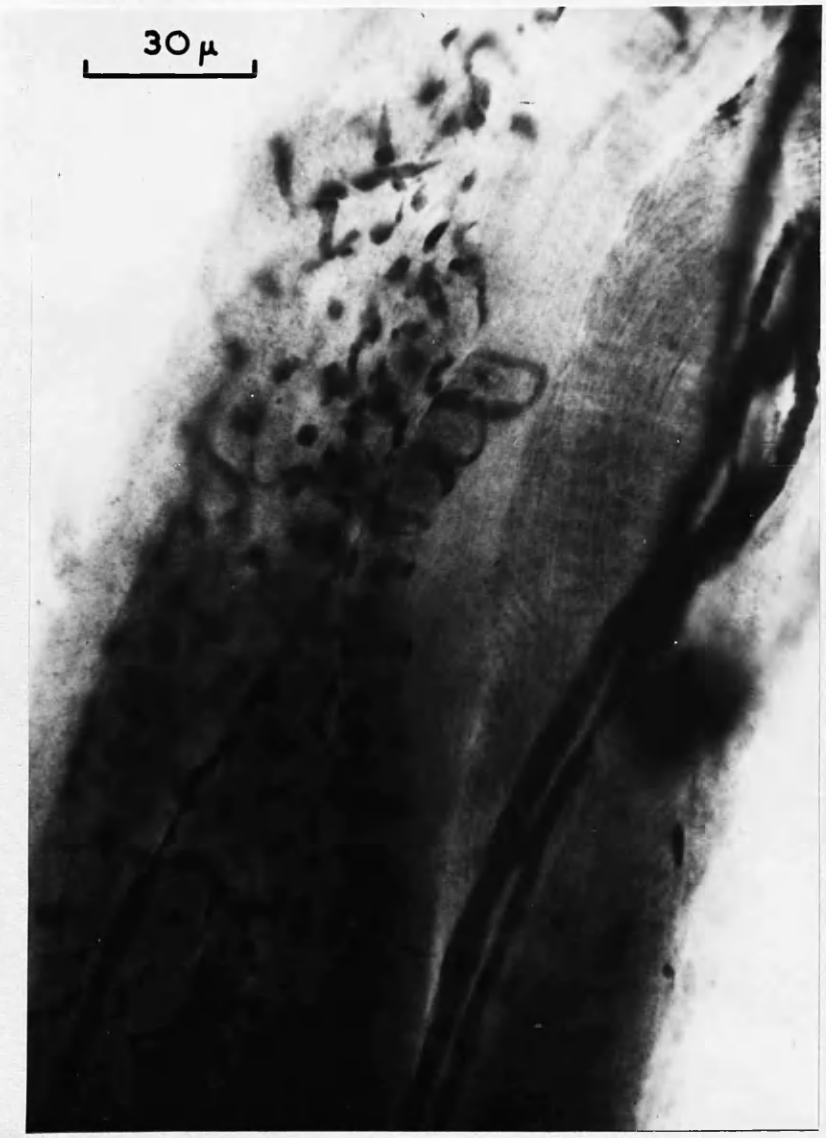



Fig. 90. Part of a muscle-spindle from the popliteus muscle at high magnification. The annulo-spiral receptors are clearly visible. (Gold chloride)


Fig. 91. Another part of the muscle-spindle shown in fig. 90. containing a flower-spray unit. A few annulo-spirals, continuations of those in fig. 90, can be seen. (Gold chloride)


Fig. 92. A simple muscle-spindle from the popliteus muscle. The spindle consists of annulo-spiral receptors only. (Gold chloride)

| Type of sensory unit | Total no. found | Sites of units |
|---|---|---|
| Spray unit | 74 | fibrous capsule |
| Lamellated unit | 12 | fibrous capsule |
| Tendon-organ | 2 | cruciate ligament |
| Muscle-spindle | 7 | popliteus muscle |

Fig. 93. Table of the total numbers of each type of sensory unit found on histological examination of tissue from 18 knee-joints, together with the sites in which these different types of unit were found to lie.

| Type of sensory unit | Dimensions of receptors (μ) | | Diameter of afferent fibre (μ) | |
|---|---|---|---|---|
| | length | breadth | fibre from single receptor | fibre from sensory unit |
| Spray | 93.8 ± 5.5 (40) | 32.8 ± 1.6 (40) | 3.9 ± 0.1 (40) | 6.3 ± 0.3 (35) |
| Lamellated | 207.2 ± 14.1 (18) | 33.1 ± 2.0 (18) | 4.3 ± 0.2 (18) | 6.4 ± 0.5 (10) |
| Tendon-organ | 500.0 (1) | 125.0 (1) | -- | 12.0 ± 0 (2) |

Fig. 94. Table of the dimensions of the receptors in the knee-joint of the cat, and the diameters of their afferent fibres as seen in specimens stained with gold chloride.

Means ± standard error. No. of observations given in brackets.

included in some of the specimens examined. The muscle-fibres were found to contain muscle-spindles of both simple and complex arrangement. Fig. 90 shows part of a complex muscle-spindle at high magnification; the annulo-spiral receptors are clearly seen. Fig. 91 shows another part of the same spindle, and here the flower-spray type of receptor can be seen; a few annulo-spirals are also visible in this photograph. In fig. 92 is shown a simple muscle spindle consisting of annulo-spiral receptors only. The tendon-fibres contained tendon-organs similar in structure to the one shown in fig. 89.

Total numbers of sensory units and comparison of dimensions

Fig. 93 is a table showing the total numbers of the various types of sensory unit encountered in the histological examination of the tissue from the 18 knee-joints. As has been mentioned earlier, the spray units are by far the most numerous.

For the purposes of comparison, the dimensions of the various types of receptor in capsule and ligament, and of their afferent fibres, are summarized in the table of fig. 94. The spray receptors are about half as long as the lamellated ones, and both are very much smaller than the tendon-organs from a ligament.

## DISCUSSION

The results show that there are two distinct types of sensory unit in the fibrous layer of the joint capsule, a spray type and a lamellated type.

It seems probable that the spray receptors described in this Thesis correspond to the Ruffini endings found in the fibrous capsule by Gardner (1944), Samuel (1948) and Sfameni (1902).

Gardner's description of the distribution, appearance and dimensions of the 'typical Ruffini endings' is in close agreement with the observations described here. He stated that the Ruffini endings were most numerous over the posterior aspect of the joint, 1 to 7 of them were supplied by the same axon, and his illustrations show the endings to be of the order of 100μ in length and 50μ in breadth (cf. fig. 94). The afferent fibres from these endings accounted for the group of axons of diameter 7μ to 10μ which comprised a large proportion of the myelinated fibres in the posterior articular nerve. One would expect these fibres to be rather less in diameter in the earlier part of their course i.e. within the capsule itself; this agrees with the dimensions of the axons to the spray sensory units given in fig. 94.

Samuel described endings which were similar in appearance to Ruffini endings, but his statement that such endings are found infrequently in normal tissue is not in agreement with the present findings.

The illustrations shown by Sfameni are of nerve-endings very

similar to the spray type of receptors in appearance. In his text, Sfameni deseribes the Ruffini endings in the periosteum of the long bones of the dog as being 640μ to 1.8mm long, 130μ to 700μ broad, and supplied by fibres of diameter 11μ to 22μ; he then states that the endings in the fibrous capsule are of the same appearance and size. However, according to the magnification given in the captions to his figures, the length of the periosteal endings shown ranges from 60μ to 200μ and the diameter of their afferent fibres ranges from 2μ to 6μ. No fibres as large as 22μ, and few larger than 11μ, are present in the articular nerves to the knee-joint of the cat (Gardner, 1944; fig. 27 of this Thesis). It seems reasonable, therefore, to suppose that the dimensions corresponding to the captions, rather than those in the text, are correct, even allowing for the fact that Sfameni used dogs for his experiments. On this basis, the size of the Ruffini endings he described is in close agreement with the dimensions of the individual spray receptors described in this Thesis (see fig. 94).

The lamellated receptors bear a certain resemblance to the larger Pacinian corpuscles found elsewhere. The simple Pacinian corpuscles referred to by Rauber (1874) and Hagen-Torn (1882) as present in the fibrous capsule of joints may correspond to the lamellated receptors described here.

Sfameni (1902) described having found, on one occasion, two oval, encapsulated endings supplied by a single axon. The illustration of these is not dissimilar to fig. 78, though his endings are rather

less elongated. The same discrepancy in scales occurs here, between text and captions, as has been mentioned above in relation to his other figures.

Cruveilhier (1841), Kölliker (1868), and Hénoque (1869) all described Pacinian corpuscles as present in or near the joints. On no occasion during the investigation reported here was a Pacinian corpuscle found in any of the capsular tissue examined. This is in agreement with the findings of more recent workers, Sfameni (1902), Gardner (1944) and Samuel (1948) none of whom found any Pacinian corpuscles within the tissues of joints. It is difficult to believe that any receptor as large as a true Pacinian corpuscle (1-4mm long: 1-2mm broad) could have escaped observation. It may be that the 'Pacinian corpuscles' described by these earlier workers were, in fact, smaller than true Pacinian corpuscles and correspond to the lamellated receptors definitely present in the fibrous capsule of the knee-joint of the cat.

Krause (1874) described end-bulbs in the synovial membrane of human interphalangeal joints. Rauber (1874) stated that these end-bulbs were in the fibrous capsule, and not in the synovial membrane. Krause described them as being almost circular, and of diameter 110μ in the dog; as more elongated, and of length 60μ to 200μ, in the rabbit. The descriptions and illustrations of Krause end-bulbs in the literature are many and varied. Some diagrams are rather similar to the photograph of a single spray shown in fig. 72, where the layers of capsule are discernable; other diagrams are more like the lamellated receptors shown in figs. 77-82 (e.g. Schäfer, 1912).

It is possible that the classification of receptors into spray or lamellated types adopted here applies to all joints, though there may be considerable variation in the detailed structure of the receptors within each class from joint to joint or species to species.

Some nerve-fibres in the fibrous capsule were found to terminate either abruptly or to taper gradually away, no organised endings being present. Examination of many of these led to the conclusion that most were not true nerve-endings at all. During dissection of the stained material it proved very easy to separate a spray from its supplying fibre at the last node before the ending; cutting through a fibre often produced an abrupt ending, or even a globular ending, the myelin spreading out at the cut end; division of a fibre by longitudinal traction gave rise to a tapered appearance of the broken ends. The existence of globular endings is therefore considered doubtful, and fibres which ended abruptly when still of considerable diameter e.g. 3μ or more, were almost certainly broken.

On several occasions a fibre was seen to divide dichotomously many times until the resultant fine branches could not be traced any further in the preparation. This type of nerve-ending is usually referred to as a 'free' ending as distinct from an 'organised' ending. Most of the 'free' endings occurred in the fatty tissue of the capsule, and few were present in the fibrous layer.

There is a small group of large fibres, of diameter 10μ to 17μ in the posterior articular nerve (see fig. 27). The finding of tendon-organs of Golgi within a cruciate ligament suggests that these

large fibres may innervate tendon-organs within the ligaments of the knee-joint. In this connection the findings of Andrew (1954, personal communication), in a study of the innervation of the medial ligament of the knee-joint of the cat, are of interest. Using a methylene blue technique, he demonstrated two types of nerve-ending; Ruffini endings lying in the connective tissue of the marginal capsule close to the medial ligament; and nerve-endings like tendon-organs of Golgi in the superficial fibres of the medial ligament. The Ruffini endings were small and were very similar to the spray receptors described here, in size and in appearance, making allowance for the differences due to the fact that different stains were employed. The Golgi nerve-endings which he described ranged in length from 150μ to 440μ, and the larger of these were very similar to the tendon-organ shown in fig. 89, which was 500μ in length and was supplied by a fibre of diameter 12μ. He did not, however, notice any appreciable difference in the sizes of the fibres supplying these two types of nerve-ending, the parent axons having diameters between 5μ and 11μ.

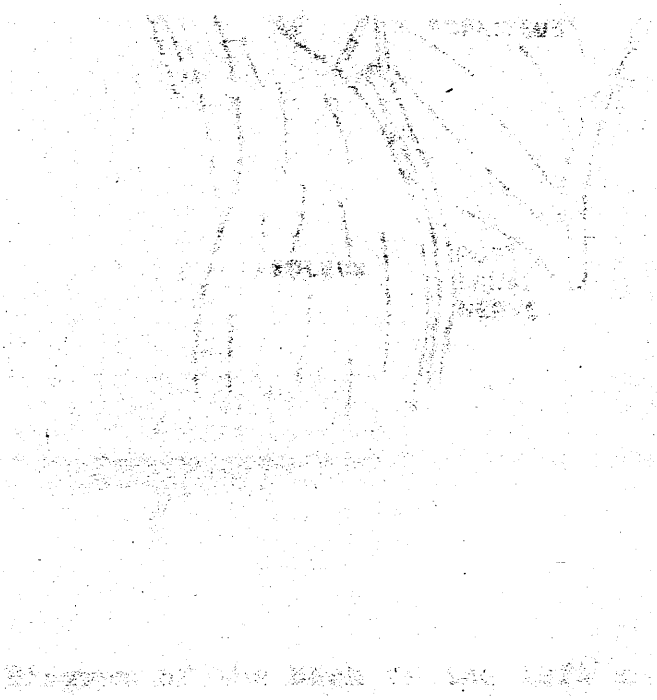
# Part 4

## THE CORRELATION OF STRUCTURE AND PHYSIOLOGICAL RESPONSE

## INTRODUCTION

In Part 2 the types of discharge to be found in the posterior articular nerve were described; these were two in number, designated 'rapidly-adapting' and 'slowly-adapting' according to the time courses of adaptation followed. In Part 3 the types of sensory unit to be found in the capsule of the knee-joint were described; these also were two in number, and were described as 'spray' sensory units and 'lamellated' sensory units because of their appearance. It seemed probable, therefore, that each of the types of sensory unit was responsible for one of the two types of discharge in the articular nerve. However, no direct correlation was possible without further information. It was hoped to gain this information by dissecting a single sensory unit from the joint-capsule while recording its discharge from a twig of the articular nerve. The units were so small, however, that this was not possible, as most pieces of capsule removed were found to contain several sensory units. It was therefore decided to dissect from the capsule a portion of it which was known to contain a sensory unit whose discharge had been analysed. The piece could then be examined histologically and the sensory

units present classified according to type. By carrying out a number of experiments of this kind it was hoped to correlate the structure of the units with their physiological response. Details of the procedure adopted have been given in Part 1, section 12. The results will now be given.



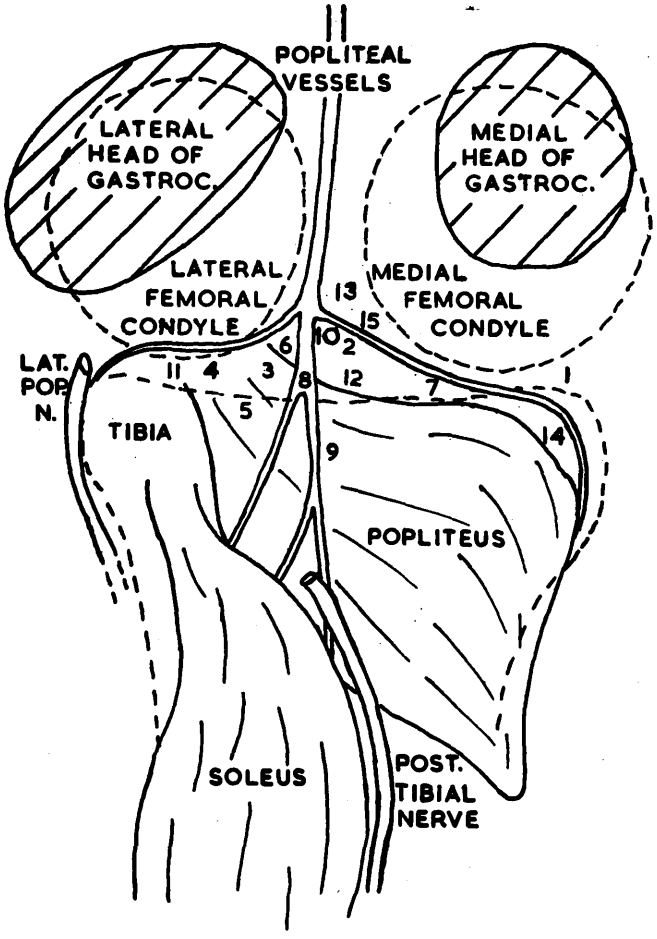



Fig. 95. Diagram of the back of the left knee-joint of the cat to show the areas from which the pieces of capsule were dissected in the 15 experiments. The area from which the specimen was removed in any one experiment is marked with the number of that experiment.

| Expt. No. | Type of response arising in the specimen | Staining of nerve-elements | | Types of sensory unit present | | | | |
|---|---|---|---|---|---|---|---|---|
| | | In specimen | In control | Spray | Lamel-lated | Tendon organ | Muscle-spindle | Unclass-ified |
| 1 | Rapidly-adapting* | Fair | Good | - | - | - | - | 2 |
| 2 | Slowly-adapting* | Good | Not examined | - | - | - | - | 2 |
| 3 | Slowly-adapting* | Fair | Good | 8 | - | - | - | - |
| 4 | Rapidly-adapting | No nerve elements | Good | - | - | - | - | - |
| 5 | Slowly-adapting* | Good | Good | ?1 | - | 2 | 4 | - |
| 6 | Slowly-adapting | Good | Good | 6 | 1 | - | - | 1 |
| 7 | Slowly-adapting | No nerve elements | Good | - | - | - | - | - |
| 8 | Slowly-adapting* | Fair | Good | 1 | 2 | - | - | - |
| 9 | Slowly-adapting | No nerve elements | Good | - | - | - | - | - |
| 10 | Slowly-adapting* | Fair | Not examined | 1 | - | - | - | - |
| 11 | Slowly-adapting | Good | Not examined | 11 | - | - | - | - |
| 12 | Slowly-adapting* | Poor | Poor | 13 | 2 | - | - | - |
| 13 | Slowly-adapting | Fair | Fair | 7 | 2 | - | - | - |
| 14 | Rapidly-adapting* | Poor | Poor | - | ?1 | - | - | ?1 |
| 15 | Slowly-adapting | Fair | Good | 2 | 2 | - | - | - |

Fig. 96. Relationship between the nature of the nervous discharges and the histological features of the sensory units. An asterisk is used to mark those experiments where it was certain that the excised portion of joint-capsule contained the sensory unit whose response had been recorded. In the other experiments there is a slight possibility that the sensory unit was not included in the portion of capsule removed.

## RESULTS

The procedure previously described, involving the removal of a piece of joint-capsule known to contain a sensory unit whose response had been analysed, constituted one experiment. Experiments were successfully completed in 11 animals; in 4 of these it proved possible to carry out the procedure for 2 units in different areas of the same capsule, thus making a total of 15 experiments.

Fig. 95 is a diagram of the back of the left knee-joint of the cat to show the positions from which the pieces of capsule were dissected in each of the 15 experiments. The area from which the specimen of capsule was removed in any one case is marked with the number of that experiment.

The histological findings in the 15 experiments are shown in fig. 96. Each specimen of capsule was usually found to contain several sensory units. In some cases, if localisation was not very precise , or when isolation of the piece of capsule containing the sensory unit had been only partially completed when the supplying nerve was severed, it was necessary to remove a larger piece of capsule to make certain that the unit, whose response had been analysed, was contained in it. These larger pieces contained correspondingly larger numbers of sensory units e.g.

Expts. 11 & 12. In cases where it was considered certain that the sensory unit whose response had been analysed was contained in the portion of capsule removed, the type of response in the table has been marked with an asterisk. In the other experiments there was just the possibility that the sensory unit was not included in the portion removed.

In two experiments (nos. 5 & 14) a sensory unit was found which was so poorly stained that definite classification was difficult, but it more closely resembled one type than the other. These units are entered in the table under the type they most closely resembled, but with a query before the appropriate figure. In four experiments (nos. 1,2,6 & 14), axons were seen to terminate in what were almost certainly sensory units, but these were either so poorly stained, or were embedded in fibrous tissue so densely stained, that identification of type was impossible; these units are entered in the table as unclassified.

For the reasons given in detail in Part 1, section 12, it may be assumed that, with the possible exceptions of experiments 11 & 12, ALL the sensory units within the specimen of capsule removed in each experiment were found and classified in the appropriate

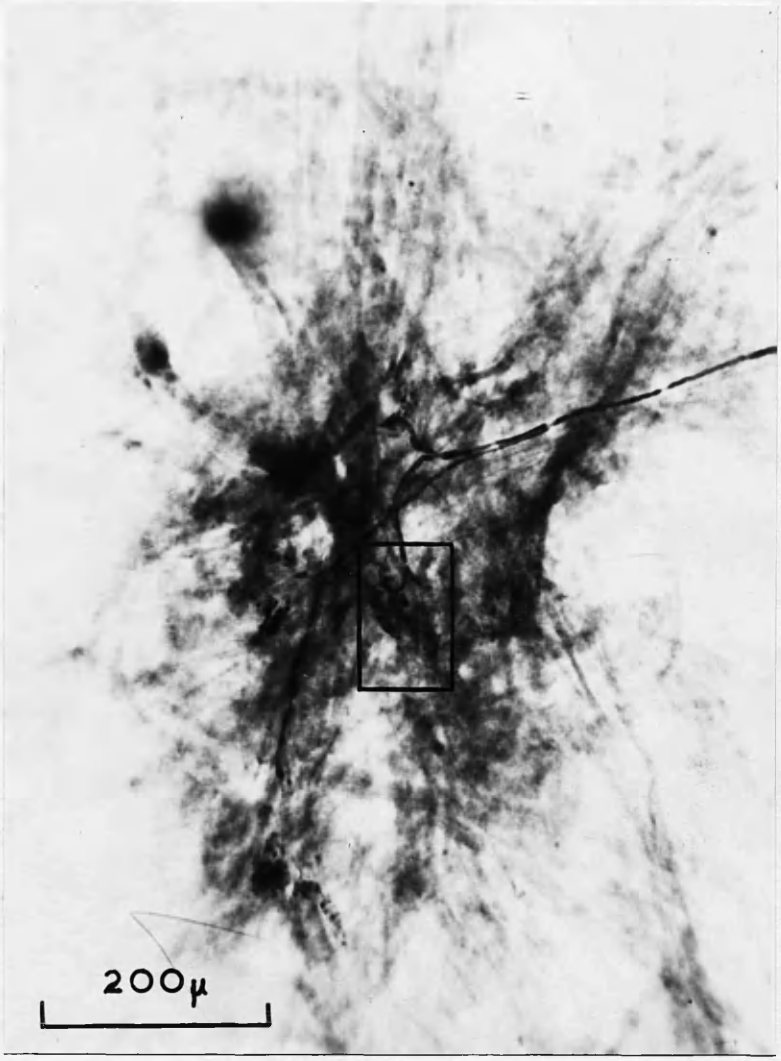



Fig. 97. A sensory unit of the spray type found in the specimen of capsule removed in Expt. 10. This was the only sensory unit present. The relationship of impulse-frequency to position of the joint for this unit is shown in fig. 99. (Gold chloride)

column of the table.

In three experiments (nos. 4,7 & 9) no nerve elements were found in the specimen. Since the staining of the motor end-plates in the control piece of muscle was good in all three cases, it is certain that there were, in fact, no nerve fibres or receptors in these specimens. In all three experiments there was, from the outset, some doubt about the presence in the tissue removed of the sensory unit responsible for the recorded discharge. This is indicated by the absence of the asterisk in the table. The sensory units are therefore not so widely distributed that any small portion of capsular tissue is likely to contain some of them. This adds significance to the cases in which sensory units were found where they were expected.

In every experiment, other than those just considered, where a slowly-adapting response had been recorded, a sensory unit of the spray type, or else one which could not be definitely classified, was present in the piece of capsule removed (nos. 2,3,5, 8,10 & 12). In one experiment (no.10), where a slowly-adapting response was obtained, the tissue examined contained only one sensory unit and it was of the spray type. This unit is shown in fig. 97; the

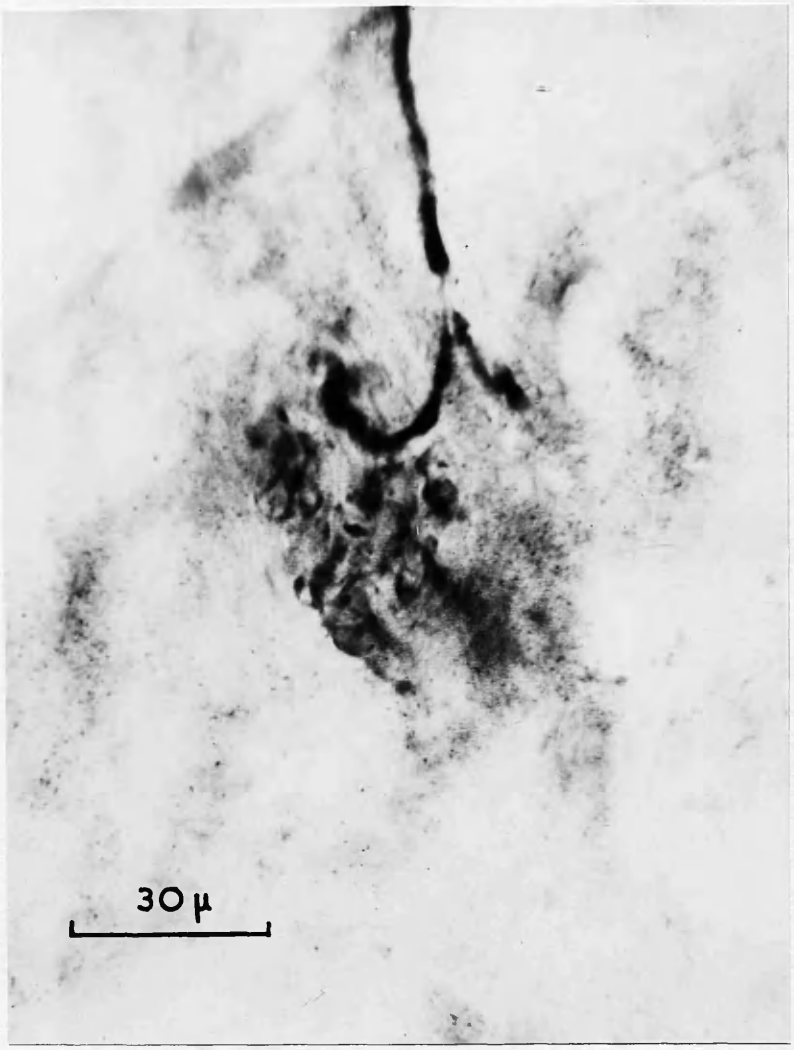



Fig. 98. The receptor outlined in fig. 97 is shown here at greater magnification. It is clearly of the spray type. (Gold chloride)

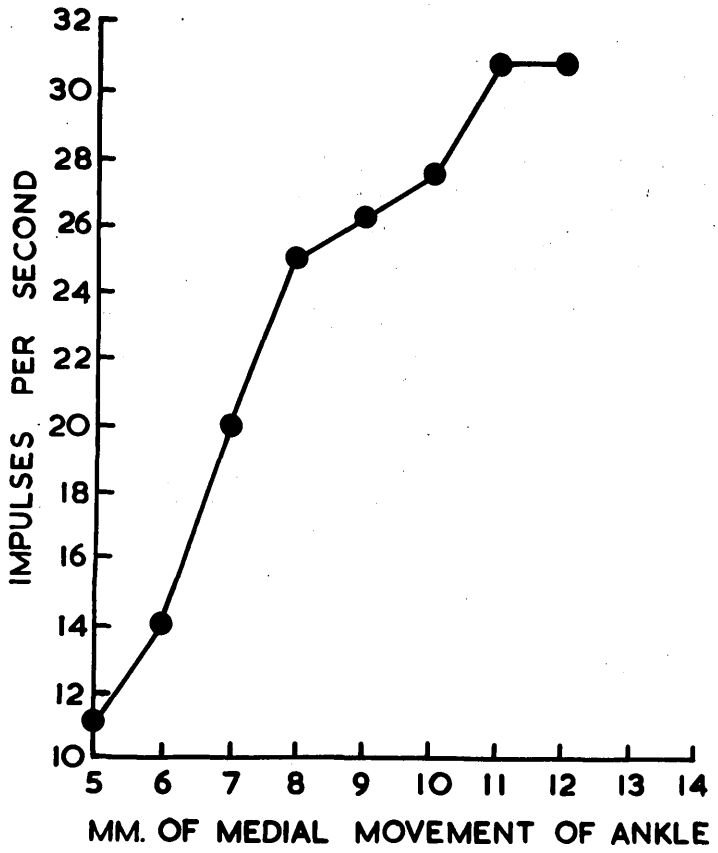



Fig. 99. Graph of the relation between adapted, steady impulse-frequency and position of the knee-joint, for the sensory unit found in Expt. 10. The unit was of the spray type (see fig. 97 & 98), and the graph is typical of the slowly-adapting type of response.

single spray within the area outlined is shown at greater magnifieation in fig. 98. The discharge localized to this piece of tissue showed the usual characteristics of a slowly-adapting response, and the relation between the position of the knee-joint and the steady, adapted frequency of discharge in each position is shown if fig. 99. The values of steady, adapted frequency were obtained after increments of movement in the direction producing an increase in impulse-frequency, as described in Part 2, section 2b.

In both the experiments in which a rapidly-adapting discharge had been definitely localized to the piece of capsule removed (Expts. 1 & 14), definite classification of the sensory units present in the specimen was not possible since the receptors were not well impregnated. In Expt. 14, however, there was a receptor similar to those of the lamellated type. An attempt to isolate it by further dissection damaged the receptor so that the final appearance was less convincing than that in the earlier stages of dissection, and photographic reproduction was not possible. This receptor, however, definitely did not belong to the spray type.

In Expt. 5, where the discharge recorded was

slowly-adapting, the excised portion of capsule had attached part of one of the cruciate ligaments and a few fibres of the popliteus muscle. The capsule proper contained one sensory unit probably of the spray type. There were two tendon-organs of Golgi in the ligament, and the muscle contained four muscle-spindles. Since it is known that the posterior articular nerve to the knee-joint does not supply the popliteus muscle (Gardner 1944; 1948), the recorded discharge cannot have come from the muscle-spindles. The discharge may, however, have arisen in one of the tendon-organs from the ligament.

It was mentioned earlier that the spray type of sensory unit is most numerous over the centre of the back of the joint-capsule, while the lamellated type tend to lie towards the sides of the joint. This is further illustrated by the fact that the specimens of capsule to which rapidly-adapting discharges had been localized (Expts. 1,4 & 14), were dissected from the areas towards the side of the joint, while the majority of the slowly-adapting specimens were taken from the centre of the back of the capsule, (see fig. 95).

## DISCUSSION AND GENERAL CONCLUSIONS

The results show that the spray type of sensory unit in the joint-capsule is responsible for the slowly-adapting discharges to be found in the posterior articular nerve. This is clear from fig. 96 which shows that in all experiments in which a slowly-adapting discharge was definitely localized to the piece of capsule removed, at least one sensory unit of the spray type, or one which was not classifiedbut which might have been of spray type, was present in the specimen (Expts. 2,3,5,8,10 & 12). In two of these experiments the spray type of sensory unit was the only type present (Expts. 3 & 10). In Expt. 10 only one spray unit was present and its response was typical of the slowly-adapting variety, there being steady impulse-frequencies appropriate to each position of the joint (fig. 99).

The lamellated sensory units are much less numerous than the spray type; the rapidly-adapting discharges are also much less frequently encountered than the slowly-adapting ones. As shown in fig. 96, when a rapidly-adapting discharge was localized to the piece of capsule removed (Expts. 1 & 14), no sensory units of the spray type were found histologically,

and in Expt. 14 one sensory unit only was found and this was probably of the lamellated type. In addition, the lamellated receptors bear a certain resemblance to Pacinian corpuscles and Pacinian corpuscles are known to give rise to rapidly-adapting discharges (Gray & Malcolm, 1950; Gray & Matthews, 1951). Since only two distinct types of sensory unit have been found, and it has been shown that the spray type is responsible for the slowly-adapting discharges, it seems reasonable to attribute the rapidly-adapting discharges to the lamellated type.

The action-potentials of the rapidly-adapting responses are almost always much larger than those of the slowly-adapting responses. The difference is more than can be accounted for by variations in the conditions at the electrodes (see Part 2). In accordance with the findings of Gasser and Grundfest (1939), it might be supposed that the rapidly-adapting responses travel inlarger fibres. However, the lamellated sensory units, which appear to give rise to these responses, are innervated by the same size of fibres as are the spray units. This apparent anomaly is interesting in view of the finding by Paintal (1953), in the vagus nerve, of large action-

potentials in fibres with a low conduction velocity, and small action-potentials in fibres with a much larger conduction velocity. It may be that the relation between fibre-size, conduction velocity and amplitude of action-potential is not as simple as was formerly thought.

Gardner (see fig. 27) has shown that the posterior articular nerve contains a large group of non-myelinated fibres of diameters less than 2μ, a large group of myelinated fibres of diameters between 2μ and 10μ, and a small group of fibres between 10μ and 17μ. The non-myelinated fibres in the nerve are concerned principally with the innervation of blood-vessels in the capsule, and some others form 'free' endings (Gardner, 1944; Samuel 1948).

The afferent fibres from both the spray and the lamellated sensory units in the capsule have diameters of the order of 6μ. It is likely that these fibres form the large group of myelinated axons less than 10μ in diameter in the articular nerve. It has already been suggested (see Part 3) that the small group of large fibres in the nerve may innervate tendon-organs within the ligaments of the knee-joint. In Expt. 5 the discharge recorded from the articular nerve was slowly-adapting in type and could have arisen in one of the tendon-organs in the specimen. Andrew (1954)

described typical Golgi tendon-organs in the medial ligament of the knee-joint ofthe cat; he also recorded afferent discharges from the medial articular nerve which supplies this ligament, and the only large-fibre discharge obtained was slowly-adapting and similar to the slowly-adapting discharges in the posterior articular nerve (Andrew 1953). Basically, the structure of the capsular spray (or Ruffini) sensory unit and the tendon spray (or Golgi) sensory unit is very similar. Each consists of a number of sprays supplied by one axon. In the Ruffini type, these sprays are orientated in three dimensions, and in the Golgi type the sprays are arranged side by side on the tendon slip, forming a more compact unit. It seems probable that both types give rise to similar slowly-adapting discharges. It may be that the Golgi sprays are designed to respond to longitudinal extension of fibres in tendon or ligament whereas the Ruffini sprays respond to the more complex deformations occurring in a joint-capsule.

The Golgi sensory units in muscle-tendons (B-organs of Matthews, 1933) give rise to slowly-adapting discharges of the same range of impulse-frequency as the slowly-adapting discharges from the capsular spray units. Both types of unit show, when the tension

on the unit is varied, a greater change in impulse-frequency than that necessary to reach the value appropriate to the new conditions. This 'exaggeration' in response is less marked with the tendon units than with the capsular units. The flower-spray sensory units in muscle-spindles (Al-organs), however, discharge with greater impulse-frequency, and show much greater exaggeration in frequency, when t he tension on the spindle is varied than do either the spray sensory units in tendons or the spray units in the joint capsule; the flower-spray units are also histologically similar, in many ways, to the other types of spray unit (fig. 91).

The differences in the responses of these various spray sensory units may be due to differences in the physical nature of the tissues in which they lie e.g. tendons, joint-capsules, and intrafusal muscle-fibres. It is suggested that the morphologically similar sensory units of spray type in the fibrous capsule of joints, in periosteum, in ligaments, in muscle-spindles and in muscle-tendons, are also functionally similar. They form a series graded in size from the small capsular units to the large units in muscle-tendons. Any differences in detailed

structure or in physiological response can be attributed to their anatomical relation to their auxiliary structures.

## SUMMARY

1. Using a 'single-fibre' technique, afferent discharges from single sensory units in the capsule of the knee-joint of the decerebrate cat have been recorded from the posterior articular nerve to this joint.

2. The responses are of two types - 'rapidly-adapting' and 'slowly-adapting'.

3. The rapidly-adapting responses consist of impulses during movement of the joint but not while the joint is stationary. Such responses were found on only a few occasions and are similar to those from the C organs of Matthews (1933), and also to those attributed by Gray & Matthews (1951) to Pacinian corpuscles.

4. The slowly-adapting responses were more frequently encountered. They are characterized by maintained steady discharges while the joint is stationary, with 'exaggerated' changes in frequency during movement. The degree of exaggeration depends on the rate of movement, and the exaggerated response is followed by adaptation to a new, steady impulse-frequency.

5. The steady, adapted impulse-frequency in any one position is independent of the rate, but not always

of the direction, of the movement used to reach that position. If the movement is one which produces a decrease in the frequency of the impulses, the final steady value may be less than that in the same position following a movement in the direction producing an increase in impulse-frequency. The degree of this 'directional' effect varies from unit to unit.

6. The sensory units giving rise to both types of response can be made to discharge by direct pressure on the part of the capsule in which they lie. By locating them in this way, the slowly-adapting units have been found to be most numerous in the centre of the back of the joint-capsule, whereas the rapidly-adapting units tend to lie towards the sides of the joint.
7. Using the Gairns (1930) gold chloride technique, two types of sensory unit have been demonstrated histologically in the posterior part of the knee-joint capsule, a 'spray' type and a 'lamellated' type.
8. By obtaining a single-fibre discharge from the articular nerve and, while still recording the discharge, excising the particular area of capsule containing the sensory unit responsible for the discharge, it has been possible to correlate the

structure of the sensory units with their physiological response.

9. The sensory units of spray type consist of a number of sprays supplied by a single axon, and are situated in the fibrous layer of the joint-capsule; they are undoubtedly the 'typical Ruffini endings' described by Gardner (1944). They are definitely responsible for the slowly-adapting discharges in the posterior articular nerve. It is suggested that these spray sensory units are capable of providing accurate information about the relative position of the bones forming the joint.

10. The lamellated sensory units, which also lie in the fibrous capsule, are much scarcer than the spray type. They consist of several receptors supplied by a single axon. These receptors are double the length of the spray receptors, but are very much smaller, and relatively more elongated, than Pacinian corpuscles. The lamellated type of sensory unit is almost certainly responsible for the rapidly-adapting discharges in the posterior articular nerve.

11. It is doubtful if other types of organised nerve-ending exist in the capsule, but some free nerve-endings are present. On one occasion tendon-organs were found in a cruciate ligament.

12. It is suggested that the larger fibres in the articular nerve innervate tendon-organs in the ligaments of the joint, and that the response of these is similar to the response of the spray sensory units in the capsule. The possibility is discussed that the capsular spray units, the sensory units of spray type (tendon-organs) in ligaments and tendons, and the flower-spray units in muscle-spindles form a series of sensory units, graded in size, which are all basically similar in structure andin function.

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