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DORSAL COLUMN PROJECTION OF FIBRES FROM THE CAT KNEE JOINT

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SUMMARY

1. Stimulation of the cervical dorsal columns excited an average of nine knee joint fibres in the cat posterior articular nerve, eleven fibres in the cat medial articular nerve and thirteen fibres in the monkey posterior articular nerve.

2. Joint fibres projecting to cervical levels were shown to be rapidly adapting by recording with micro-electrodes from single fibres in intact cat posterior articular nerves. The numerous slowly adapting fibres could not be antidromically excited from the cervical dorsal columns.

3. Several control experiments suggested that the antidromic stimulation method accurately defined the dorsal column projection of joint fibres.

INTRODUCTION

Joint afferent fibres are generally believed to enter the dorsal columns and project without interruption to the dorsal column nuclei (Brodal, 1948; Rose & Mountcastle, 1959). This concept has been derived mainly from testing human subjects with defects in position sense resulting from spinal cord damage. Such studies are difficult to interpret because inadvertent spinal lesions are rarely confined to one tract or a single sensory system (Head & Thompson, 1906; Brodal, 1948). In addition, the results of controlled dorsal column lesions in man and animals are conflicting; some reports indicate a profound deficit in position sense (Ferraro & Barrera, 1934; Gilman & Denny-Brown, 1966), others little or none (Cook & Browder, 1965; Vierck, 1966).

Cells influenced by joint movement have been described in the dorsal column nuclei, but they have not been found in great numbers (Gordon & Paine, 1960; Kruger, Siminoff & Witkovsky, 1961; Perl, Whitlock &

Gentry, 1962; Winter, 1965). Furthermore, there is evidence that they predominate rostrally in the nucleus gracilis (Kuhn, 1949; Winter, 1965), a portion of the nucleus which seems to possess less obvious 'lemniscal' properties than more caudal regions (Gordon & Jukes, 1964). The persistance of cortical potentials from joint nerves after section of the dorsal columns (Gardner & Noer, 1952; Gardner & Haddad, 1953) is also consistent with the idea that information from joints reaches higher centres by pathways other than the dorsal column–medial lemniscal system.

In the present experiments, we attempted to determine the fraction of posterior and medial articular nerve fibres projecting to cervical levels via the dorsal columns and to define the characteristics of both projecting and non-projecting fibres. An approach utilizing micro-electrodes to record the activity of single fibres in uncut peripheral nerves was used (Burgess & Perl, 1967; Petit & Burgess, 1968). With this technique, both antidromic and orthodromic activity in a fibre could be recorded, allowing a study of receptor characteristics, determination of conduction velocity and testing for central projection through the dorsal columns.

METHODS

Twenty-five experiments were done on cats and four on young adult squirrel monkeys. The animals were anaesthetized with sodium pentobarbitone (Nembutal, Abbott Laboratories) and given supplemental doses as needed. End-tidal CO_2 was monitored continuously and carotid arterial blood pressure was measured in the cat. Rectal temperatures were maintained at 37·5 $\pm$0·2° C with external heat, and a lamp was usually used to warm the hind limb.

In experiments requiring electrical stimulation of the spinal cord or peripheral nerves, gallamine triethiodide (Flaxedil, American Cyanimid) was used to immobilize the animal. Periodic administration of sodium pentobarbitone was continued in amounts sufficient to maintain complete anaesthesia. The animals were artificially respired with air and the respirator was adjusted to maintain end-expiratory CO_2 levels between 4 and 5%. The animals were rigidly mounted in a frame in the prone position. Some experiments required rigid fixation of the extended hind limb which was accomplished with a steel pin driven into the tibia and by holding the foot with a clamp.

Gross recording from the knee joint nerves. In the cat, either the posterior articular nerve or the medial articular nerve was used for the gross recordings of antidromic activity evoked by dorsal column stimulation. The posterior nerve was used in the monkey. The nerves were partially freed from surrounding connective tissue and placed on platinum wire recording electrodes. A short laminectomy was done at the cervical level (C2–C3) to expose the spinal cord. A rounded platinum electrode (cathode) 1 mm in diameter was placed on the intact dura and the anode attached to surrounding tissue. In early experiments, results were compared using the surface electrode on the dura, the same electrode directly on the cord dorsum, a pair of platinum wires inserted into the cord to straddle the ipsilateral dorsal column, and bipolar stimulation of the dorsal columns dissected free from the spinal cord. As in similar studies on cutaneous afferent projections (Petit & Burgess, 1968), no significant differences were observed. Each response was tested at repetition rates of 10/sec or more to minimize dorsal root reflexes (Toennies, 1938). Conduction distance was determined *in situ* by

measuring a thread laid along the vertebral canal and peripheral nerve between the stimulating and recording points.

Gross recording from the dorsal columns. In several experiments, gross recordings from the dorsal columns were made for the purpose of comparing orthodromic and antidromic activity in primary afferent fibres from the posterior articular nerve. The posterior articular nerve was dissected free, cut and the central end placed on one platinum wire electrode for stimulation or recording. The indifferent electrode was connected to surrounding tissue. In a few experiments, the sciatic nerve was also prepared for recording in order to monitor the input volley. Supramaximal shocks were used in all tests.

The mid thoracic dorsal columns were exposed and the dura was opened. Two sharpened tungsten electrodes were inserted about $\frac{1}{2}$ mm deep into the ipsilateral dorsal column for stimulation or recording. Orthodromic records were obtained by stimulating the peripheral nerve while recording from the dorsal column, and antidromic records were obtained by reversing the procedure.

Responses evoked by articular nerve stimulation were averaged with a Fabri-Tek 1062 computer. Memory contents were either displayed on an oscilloscope and photographed or more often printed out on an X–Y plotter. The stimulation rate was 10–18/sec.

Micro-electrode recording from the posterior articular nerve. Before micro-electrode recording was begun, gross potentials from the posterior articular nerve were obtained by stimulating the intact sciatic nerve (pulse durations 0·1–0·2 msec) to determine the stimulus intensity required to excite all myelinated fibres. The gross recording electrodes were then removed and the nerve was placed on a small lucite platform in preparation for micro-electrode recording. The methods employed have been described in detail previously (Petit & Burgess, 1968). In order to know when the micro-electrode approached a nerve fibre, the sciatic nerve was stimulated twice per second while the electrode was advanced. Peripheral conduction velocities were calculated from electrical response latencies (sciatic stimulation) at slightly suprathreshold and three times threshold stimulus strengths and the conduction distance measured *in situ*. Conduction distances were usually greater than 5·5 cm. No allowance was made for utilization time at the stimulating electrode. Only slight shifts in latency (0·05–0·1 msec) were observed between just suprathreshold and thrice threshold shocks with the 0·1–0·2 msec stimulus pulse durations used.

Each posterior articular nerve fibre isolated was tested for dorsal column projection and its receptive properties were examined by manipulating the joint. Due to the location of the posterior articular nerve and the mechanical stability required for micro-electrode recording, it was not possible to move the leg. The receptors were activated either by gentle tapping or probing about the knee or by inflation of the joint capsule. For the latter, two 18 gauge needles were inserted into the posterior joint cavity from the anterior aspect of the knee. One was connected via a length of polyethylene tubing to a syringe filled with warm mineral oil. The other needle served as a drain cannula or was connected to a pressure transducer. The activity recorded in these experiments and those described below was expressed as 'instantaneous' firing rate versus time. The instantaneous firing rate was obtained using an electronic circuit which measured successive interspike intervals (expressed in seconds) and plotted their reciprocals.

Recording from dorsal root filaments. Six experiments were carried out to compare the responses of joint receptors to local mechanical stimulation and joint movement. Dorsal root recordings from single posterior articular nerve fibres were made using methods described in the previous paper. Each fibre was tested both with joint movement over the entire physiological range and with the same inflation-tapping-probing technique used to activate receptors in the micro-electrode studies.

Micro-electrode recording in the dorsal columns. In four experiments, the eighth to tenth thoracic segments of the spinal cord were exposed in preparation for micro-electrode recording. A bilateral pneumothorax and a dural hammock were used to stabilize the cord. The

same micro-electrodes and recording methods were used as with the posterior articular nerve. The sciatic nerve was stimulated twice per second at a strength supramaximal for myelinated fibres while the micro-electrode was advanced through the ipsilateral dorsal column. When a fibre driven from the sciatic nerve was located, various physiological stimuli were used to identify the receptor type.

Histology. Most of the articular nerves were prepared for histological examination as described in the accompanying paper.

RESULTS

Activation of afferent fibres from the joint by dorsal column stimulation

Gross recordings. The posterior and medial articular nerves are small enough that unitary activity from most myelinated fibres can be seen in recordings from whole nerves. In sixteen cats, the dorsal columns were stimulated at C2 or C3, and four to fifteen separate action potentials were observed in each posterior articular nerve (Table 1). The latencies of these projecting fibres fell into a narrow range and usually two or even three coincident responses were present. These could be distinguished by varying the dorsal column stimulus intensity. In four cats, the medial articular nerve was similarly tested. The medial nerve was present as two distinct branches, one on either side of the genu suprema vein. In each animal, the smaller branch on the anterior side had from one to four responding fibres, the larger branch seven to eleven fibres (Table 1).

In four monkeys, the homologue of the posterior articular nerve was prepared using Gardner's (1948) description of the human knee joint innervation as a guide, and tested from the dorsal columns. The results were comparable to those already described for the cat, with from eleven to sixteen fibres responding to dorsal column stimulation in each animal (Table 1).

The posterior articular nerve in the cat contains approximately 180 myelinated fibres (Fig. 1*b*) and is nearly the same size as the medial nerve in the cat and the posterior nerve in the monkey. Thus a relatively small fraction of the fibres in these articular nerves project to cervical levels via the dorsal columns.

Micro-electrode recording in the posterior articular nerve

Adequacy of the sample. A total of 478 posterior articular nerve fibres were examined for dorsal column projection. This population is unselected in the sense that every fibre providing a stable potential has been included. Although recordings were usually made in a systematic fashion across the nerve, duplication, i.e. recordings from the same fibre more than once, was observed on occasion. Many fibres, especially the projecting ones, had sufficiently distinctive properties so that duplication could be recognized and ten obvious duplicates were eliminated in the final tally.

Figure 1*a* shows the frequency of occurrence of fibres in the micro-electrode sample as a function of conduction velocity. Figure 1*b* is a histogram of fibre diameters from ten nerves. No correction was made in Fig. 1*b* for possible dimension changes resulting from the histological procedures (Williams & Wendell-Smith, 1960). The histograms of the micro-electrode and histological samples have the same general shape except for some

TABLE 1. Articular nerve fibres activated by cervical dorsal column stimulation

		Number of fibres in each experiment
Posterior articular nerve		
Cat (16 expts.)	Max.	15
	Min.	4
	Mean	9
	S.D.	3·1
Monkey (4 expts.)	Max.	16
	Min.	11
	Mean	13
	S.D.	1·1
Medial articular nerve (includes both branches)		
Cat (4 expts.)	Max.	14
	Min.	8
	Mean	11

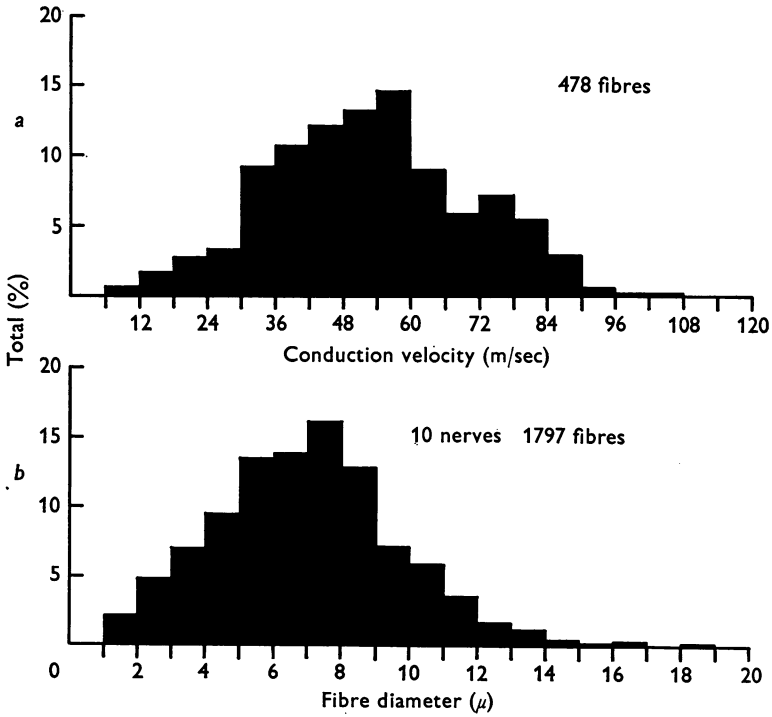

Fig. 1. Frequency of occurrence distributions of (*a*) conduction velocities in micro-electrode sample and (*b*) fibre diameters in histological sample. Posterior articular nerve.

apparent bias in the micro-electrode population for large fibres. A bias favouring large fibres had been observed earlier in a micro-electrode study of cutaneous fibres (Burgess, Petit & Warren, 1968). A comparison of results from individual experiments (Fig. 2) shows a similar over-all agreement in the shape of the histograms from micro-electrode and histological samples.

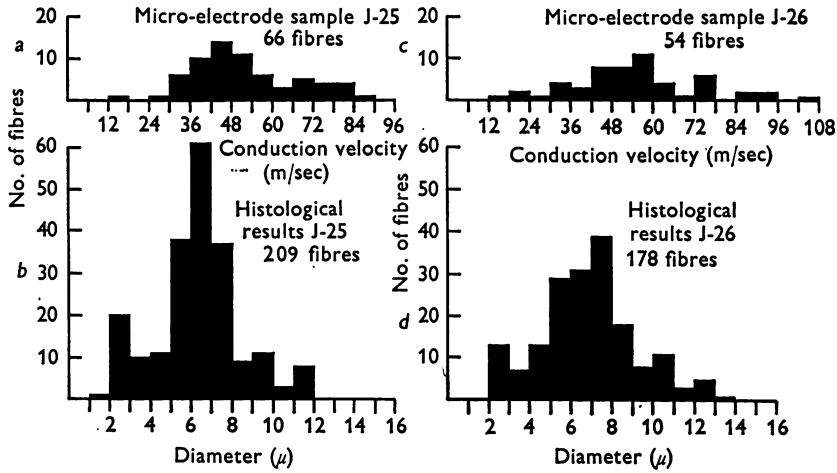

Fig. 2. Frequency of occurrence histograms of conduction velocities in micro-electrode samples, (*a*) and (*c*), and fibre diameters, (*b*) and (*d*). Two separate experiments. Posterior articular nerve.

Receptor characteristics. Inflation of the capsule with mineral oil plus tapping and probing about the knee were used to activate joint receptors in the peripheral nerve micro-electrode experiments because the stability required for micro-electrode recording prevented movement of the leg. Since these were the only methods available for determining the properties of individual projecting and non-projecting fibres, it was desirable to determine whether such artificial stimuli elicited the same type of response from joint receptors as joint movement. Five experiments were performed to compare the responses of individual receptors to both types of stimulation.

In all, sixty-four fibres were studied. Of these, thirty-six responded with a sustained discharge at both flexion and extension and were classified as flexion–extension fibres (see accompanying paper). Two other fibres responded with a sustained discharge only near maximum extension and were classed as extension types. Both the flexion–extension and extension fibres responded to capsule inflation with a rhythmic sustained discharge that persisted for as long as capsule pressure was elevated (Fig. 3*a*) and small fluctuations in capsule pressure revealed a sensitivity to the rate at which the pressure was changed (Fig. 3*b*).

Four fibres responded to joint movement only in flexion and were classed as flexion fibres. Twisting the tibia 'outward' so as to abduct the foot caused these receptors to respond over nearly the entire flexion–extension range, and 'inward' twist inhibited the response. Two of the flexion fibres had peripheral conduction velocities between 80 and 85 m/sec. The first responded weakly to capsule inflation with a phasic discharge. The second

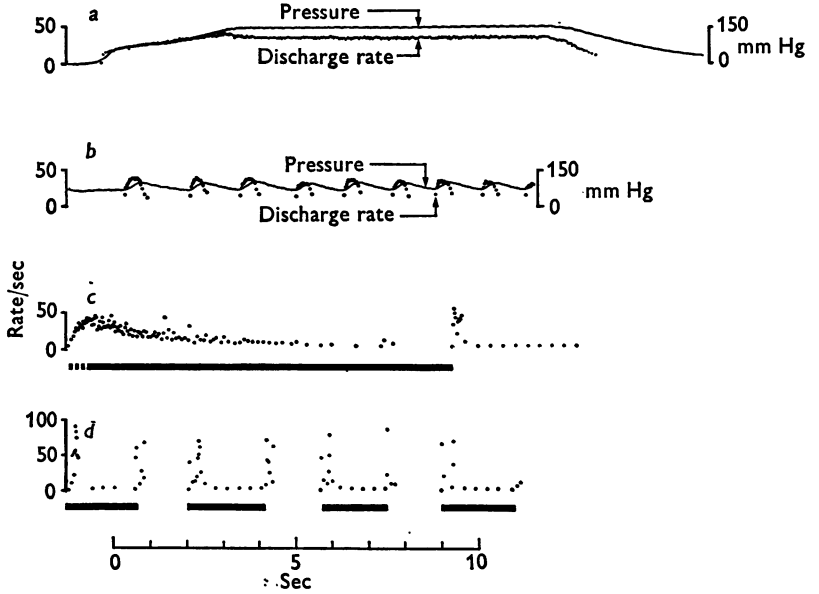

Fig. 3. Response of joint receptors to capsule inflation. 'Instantaneous' firing rate has been plotted versus time. Instantaneous rate calculated from time intervals between successive pairs of impulses and marked by a dot placed along the time axis (horizontal) at the instant of the second impulse for each calculation. Response of slowly adapting receptor to (*a*) steady pressure and (*b*) pressure fluctuations below the level required for sustained discharge. (*c*) represents phasic joint receptor response during increasing pressure (interrupted line) and steady pressure (continuous line). When pressure was released, the receptor responded with a transient discharge and followed the pulse. (*d*) shows corpuscle-like receptor response to pressure suddenly applied, held and released. The continuous line indicates the duration of the stimulus. The receptor discharged in synchrony with the pulse during sustained pressure.

fibre was not activated by inflation. The remaining fibres had axon conduction velocities of 39 and 48 m/sec and both were tonically active when tested. The discharge rate of the 39 m/sec fibre was enhanced by gentle capsule inflation and inhibited by stronger inflation. The response of the 48 m/sec fibre was unaffected by inflation.

Six fibres supplied phasic joint receptors. When these receptors were excited by inflating the capsule (Fig. 3*c*), the discharge produced was

similar to that obtained by moving the joint or by pressing on the side of the knee (see accompanying paper).

One receptor was identified as Pacinian corpuscle-like (Gray & Matthews, 1951; Hunt, 1961). It was sensitive to slight movement of the knee in either direction and to tap, responding with a phasic burst of activity as described in the accompanying paper. A transient response to increasing or decreasing capsule pressure was readily obtained, and with a constant elevated pressure the receptor discharged in synchrony with the pulse (Fig. 3*d*).

TABLE 2. Summary of micro-electrode sample

Receptor type	Number of fibres (468 total)		Activated antidromically by cervical dorsal column stimulation
Slowly adapting	210	45 %	No
Rapidly adapting	40	8·6 %	Yes
	28	5·9 %	No
Responded only to extreme procedures	4	0·9 %	No
Not identified	186	39·8 %	No

One 27 m/sec fibre responded tonically at intermediate joint angles, but was not activated by inflation. Three fibres with conduction velocities of 10, 20 and 28 m/sec responded only to extreme extension or strong capsule inflation, which was probably noxious. These slowly conducting fibres responded to both types of stimulation with a low frequency (less than 15/sec) maintained discharge which persisted for 5–10 sec after the stimulus was terminated. Six fibres discharged tonically to both joint movement and inflation and three fibres were rapidly adapting to both procedures. Further identification was not made. The remaining two fibres could not be activated by any procedure employed.

Thus, if activated, most receptors respond similarly to capsule inflation, externally applied pressure and joint movement. This is most obvious in the case of rapidly adapting receptors and those with a slowly adapting discharge at extension. Flexion receptors are apparently difficult to excite by capsule inflation.

Projecting fibres. Four hundred and sixty-eight (after deleting ten obvious duplicates) posterior articular nerve fibres were tested from the cervical dorsal columns, and forty (8·6 %) could be antidromically excited (Table 2). During the test for dorsal column projection, a wide range of stimulus intensities and durations was used to minimize the chance that a projecting fibre might escape activation. The projecting fibres always had low thresholds to dorsal column stimulation. All forty projecting fibres were identified as originating from receptors that were predominantly or exclusively rapidly adapting. About one half were further classified, and

of these 60 % were Pacinian corpuscle-like and the remainder were of the phasic joint type. All corpuscle-like receptors identified in the nerve were found to project, whereas over half the phasic joint receptors did not.

The peripheral conduction velocities of the projecting fibres fell between 52 and 84 m/sec (Fig. 4*a*). In individual experiments the range was considerably less, and it was not unusual to have two or more projecting fibres with the same conduction velocity, as anticipated from the results obtained

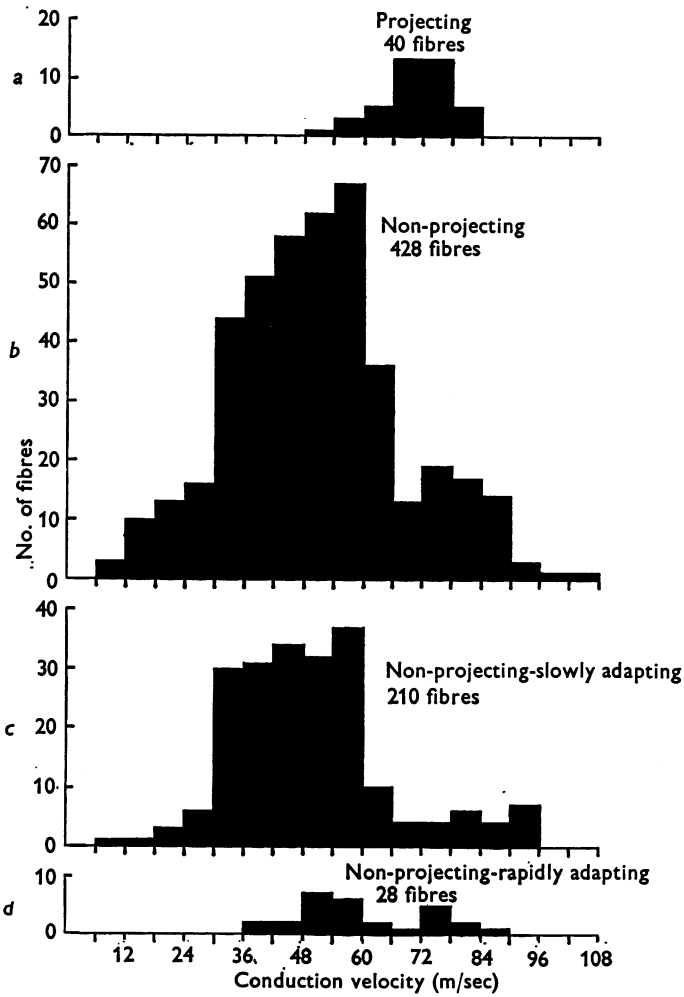

Fig. 4. Frequency of occurrence versus conducting velocity for the various classes of fibres studied in the posterior articular nerve. All projecting fibres (*a*) were identified as completely or predominantly rapidly adapting. Of the non-projecting fibres (*b*), 210 (*c*) were slowly adapting, and 28 (*d*) had rapidly adapting characteristics. The properties of the remaining non-projecting fibres were not determined (see text).

with gross recordings. There was no obvious difference in the conduction velocities of the phasic joint and corpuscle-like receptor fibres.

Non-projecting fibres. A total of 428 non-projecting posterior articular nerve fibres were observed, representing 91·4 % of the total micro-electrode sample (Fig. 4*b*). One hundred and eighty-six of these non-projecting fibres were unidentified because they could not be activated with the natural stimuli available or could not be tested adequately due to stability problems with the micro-electrode (Table 2). Apparently, the position of the hind limb had some influence on the number of excitable receptors. Rigid fixation with flexion 15 to 20° from maximum extension without twisting the tibia, seemed to give the best yield. The number of unidentified fibres decreased as care was taken in positioning the limb and avoiding strong capsule inflation. In the later experiments, the receptor properties of over 90 % of the fibres encountered could be determined.

Of the 242 identified non-projecting fibres, 210 were slowly adapting; i.e. receptors which responded readily to capsule inflation with a persistent regular discharge (Fig. 3*a*). A few were spontaneously active, in which case capsule inflation caused an increase or, on rare occasions, a decrease in the discharge rate. The conduction velocities of all identified slowly adapting fibres are shown in Fig. 4*c*.

Twenty-eight non-projecting fibres were rapidly adapting (Fig. 4*d*). Thirteen of these were studied sufficiently for identification and all were of the phasic joint type. Four non-projecting fibres conducting in the 8–30 m/sec range responded only at the maximum inflation used.

Adequacy of the method used to test for dorsal column projection

The experiments reported above using antidromic stimulation suggest that relatively few knee joint afferent fibres project via the dorsal columns. However, in order for the antidromic method to be satisfactory, the technique used for dorsal column stimulation must activate all projecting fibres. Furthermore, there must be no block in the conduction of antidromic activity at fibre branch points or at any other location along the path from the cervical dorsal columns to the peripheral recording site. Several control procedures were used to test these possibilities.

In experiments using a variety of electrode configurations, stimulus strengths and durations, in no case was it possible to excite more fibres than could be activated by an electrode placed on the intact dura. Among the procedures tried were a surface electrode placed directly on the cord dorsum, a bipolar needle electrode inserted into the spinal cord straddling the ipsilateral dorsal column, and a monopolar needle electrode on the surface or penetrating the columns to different depths at various locations.

In several experiments the dorsal columns at the cervical level (C2–C4)

or more often at thoracic levels (T 7–T 9) were dissected free from the spinal cord and placed upon bipolar electrodes for stimulation. The same posterior articular nerve fibres were always activated by stimulating the dissected dorsal columns and by an electrode placed on the dura. A shallow cut made through the ipsilateral dorsal column a few cm caudal to the point of stimulation invariably abolished the antidromic activity recorded in the posterior nerve.

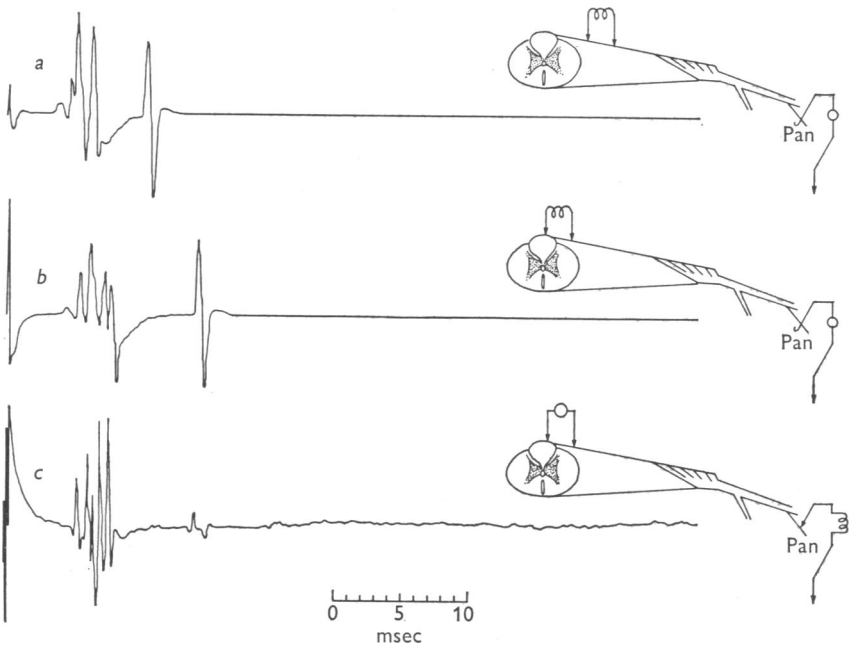

Fig. 5. Posterior articular nerve (Pan) fibres which project via the dorsal columns to mid thoracic levels. The rapidly conducting group in each record contains seven fibres, the slower potential is from a single fibre. (*a*) shows posterior articular nerve response to dorsal column stimulation. Conduction distance 380 mm. (*b*) shows posterior articular nerve response with dorsal column electrode 31 mm rostral to position in (*a*). (*c*) shows dorsal column response to posterior articular nerve stimulation.

Two control procedures were used to test for the possibility that a block of antidromic activity in the dorsal columns may have prevented the detection of projecting fibres. The first compared the posterior articular nerve response to dorsal column stimulation at T 7–T 9 (antidromic test) with the dorsal column response at this same level to posterior articular nerve stimulation (orthodromic test). For the orthodromic test, many responses were averaged to improve the signal to noise ratio. In Figs. 5*a* and *b* the activity is conducted antidromically, in Fig. 5*c* orthodromically.

By varying the intensity of the electrical stimulus, seven fibres could be recognized in the rapidly conducting group shown in Fig. 5. The slower potential was from a single fibre. A comparison of Figs. 5*a* and *b* shows that the slower conducting fibre had a velocity of 7 m/sec in the thoracic region, and indicates that fibres conducting slowly in the dorsal columns can be detected with antidromic stimulation. This fibre could not be excited by stimulating the dorsal columns at the cervical level although the more rapidly conducting group was. When the dorsal columns are stimulated caudal to the cervical cord, additional posterior articular nerve fibres with longer latencies are activated, the first of these usually appearing at mid-thoracic levels. A comparison of Figs. 5*a* and *b* with Fig. 5*c* indicates that the same population of fibres conducted in both the antidromic and orthodromic directions. Activity was never noted in orthodromic records which could not be seen with the antidromic method.

As a further control, the dorsal columns were explored with micro-electrodes for primary afferent joint fibres. Of the 134 fibres studied at T 9–T 10, only one was associated with the knee or ankle joints; it was of the Pacinian corpuscle type. Four additional fibres were tonically activated by manipulation of a single claw. Flexion or extension of the claw was effective in producing a response, but less so than twisting. Manipulation of the other toe joints produced no activity. Receptors of this type have been studied with micro-electrodes in the plantar nerve and were found to be antidromically activated by cervical dorsal column stimulation (P. R. Burgess & D. Petit, unpublished). Activity of this sort has also been described in the dorsal column nuclei (Gordon & Jukes, 1964). The results of the dorsal column recording experiments are therefore consistent with the data obtained by the antidromic method.

DISCUSSION

Apparently relatively few fibres from the posterior and medial articular nerves in the cat and the posterior articular nerve in the monkey project to cervical levels via the dorsal columns. Furthermore, only fibres from rapidly adapting receptors were found to project. Evidence that the antidromic method provides a satisfactory test for dorsal column projection comes from several control experiments. A variety of dorsal column stimulating procedures were used without altering the population of antidromically excited fibres. Recordings from single fibres in the dorsal columns failed to yield any number of slowly adapting joint fibres, except from the terminal phalangeal (claw) joints. Finally, records obtained by alternately stimulating and recording from the posterior articular nerve and the dorsal columns never revealed orthodromic activity which was not also pro-

pagated antidromically. The method of signal averaging employed permitted identification of fibres conducting orthodromically as slowly as 10 m/sec in the thoracic dorsal columns. Although it is not possible to exclude the presence of a few unobserved knee joint fibres projecting the length of the dorsal columns, it is not likely that a significant population of such fibres exists.

The need for stability while recording with micro-electrodes from fibres in the posterior articular nerve restricted methods of joint receptor excitation to capsule inflation and pressing or tapping on joint structures. By recording joint fibre activity in dorsal root filaments, inflation was found to excite all slowly adapting receptors which responded when the knee was extended, but less reliably receptors of the flexion type. Some or all of the latter may be included in the population of unidentified non-projecting fibres. In contrast, all projecting fibres were identified as rapidly adapting. Every identified Pacinian corpuscle-like receptor projected, but more than 50 % of the phasic joint receptors could not be activated from the cervical dorsal columns. Gardner, Latimer & Stillwell (1949) also show relatively few projecting fibres with gross recording from the posterior articular nerve during dorsal column stimulation. Recent studies (Petit & Burgess, 1968; see also Brown, 1968) have indicated that more than 80 % of the fibres projecting to cervical dorsal column levels from the cat sural nerve supply rapidly adapting receptors. Thus, the dorsal column system primarily mediates the activity of rapidly adapting receptors from both the skin and knee joint.

It is possible that the posterior articular nerve fibres studied in these experiments are not directly concerned with position sense, and that the fibres primarily involved supply the knee joint and adjacent structures through other nerves. Such hypothetical fibres might respond more specifically at intermediate angles, for example, than the population described in the preceding paper. If such fibres exist they must be tested for dorsal column projection before the role of the dorsal columns in position sense can be evaluated. Nevertheless, the observation that many articular fibres do not project to cervical levels via the dorsal columns casts doubt upon the validity of the classical concept that the dorsal columns are an essential pathway for position sense. Experiments in which the activity of single cortical cells was recorded (Mountcastle & Powell, 1959), have shown that neurones at this level are influenced by joint movement, but provide no information concerning the spinal pathways involved. The work of Perl & Whitlock (1961) has shown that thalamic cells in the nucleus ventralis lateralis can respond to hind limb joint movement after dorsal column transection, results which are consistent with our findings. The spinal destination of tonic knee joint fibres and the ascending

systems they influence are not known, but preliminary experiments (F. J. Clark, unpublished) have shown that many leave the dorsal columns at lower thoracic and upper lumbar levels, the region of the hind limb projection to Clarke's column (Lloyd & McIntyre, 1950).

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