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Afferent Fibres from Muscle Receptors in the Posterior Nerve of the Cat's Knee Joint

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Summary. The properties of some receptors with afferent fibres in the cat's posterior knee joint nerve have been examined, especially those discharging tonically with the joint in intermediate positions between full flexion and extension. Some of these receptors behave like muscle spindles, and respond to manoeuvres which stretch popliteus muscle. Both in single unit and whole nerve recordings their discharge pauses during a popliteus twitch, and can be strikingly augmented by tetanic stimulation of a number of popliteus fusimotor fibres isolated from ventral root filaments. The action of succinylcholine on these receptors closely resembles its effect on popliteus spindle units with fibres sited normally in the popliteus nerve. Other units with properties suggesting origin from popliteus tendon organs were also observed; their fibres and those of the spindle units conducted at Group I velocity. It is concluded that some afferent fibres from popliteus spindles and possibly tendon organs commonly pursue an aberrant course in the posterior articular nerve of the knee joint.

Key words: Muscle afferents – Joint nerve – Popliteus spindles.

A role for signals from joint receptors in kinaesthesia, including the awareness of position and movements of the limbs, has been generally accepted since the turn of the century (e.g., Sherrington, 1900). Indeed, since the first electrophysiological studies of joint receptors (e.g., Boyd and Roberts, 1953; Skoglund, 1956), the view has gained credence that impulses from joints provide the predominant input responsible for kinaesthesia. This notion developed because joints appeared to be equipped not only with phasic endings responding to movements, but also with a population of tonic receptors capable of generating impulse patterns characteristic of any joint-angle; and because impulses from muscle stretch receptors were not then believed to project to the cerebral cortex (Mountcastle and Powell, 1959; Rose and Mountcastle, 1959).

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Furthermore, severe impairment of kinaesthesia was produced by local anaesthesia of distal joints in human subjects (Browne et al., 1954; Provins, 1958).

However, re-examination of the properties of a large population of receptors in the cat's knee joint has called in question the ability of tonic receptors to signal steady joint angle over the whole range of movement. Burgess and Clark (1969) and Clark and Burgess (1975) reported that the great majority of slowly adapting receptors with fibres in the cat's posterior articular nerve of the knee joint respond only at full flexion or full extension or to both. They also suggested that the small number of slowly adapting units which responded at intermediate angles of the joint might actually be spindle receptors in the popliteus muscle, rather than endings in the joint capsule, because their discharge was increased by small intravenous doses of succinylcholine, as well as by manipulating the popliteus muscle. Recently, this view has been disputed on the basis that removal of the popliteus muscle does not change the mean number of spontaneously discharging mid-range units seen in the whole nerve, and that succinylcholine increases the firing rate of receptors in the joint capsule proper (Ferrell, 1977). The experiments described in this paper provide definitive evidence that afferent fibres from popliteus spindles are indeed commonly present in the cat's posterior articular nerve. A preliminary account of this finding has already appeared (McIntyre et al., 1977).

Methods

The experiments were carried out on 15 cats weighing from 2.1–4.8 kg, anaesthetised with pentobarbitone given intraperitoneally in initial dosage of 35 mg/kg. Further doses were given intravenously as required. The dissection involved, initially, exposure and interruption of all branches of the femoral and obturator nerves. Laminectomy was then performed to expose the lumbosacral region of the spinal cord, and the L6, L7, and S1 dorsal and ventral roots were cut centrally. All branches of the sciatic nerve were then severed, except for the posterior articular nerve (PAN) of the knee joint, and the nerve to popliteus. Completeness of the denervation was checked by stimulating whole ventral roots. The PAN and popliteus nerves were dissected free of surrounding tissues, and mounted on electrodes in a paraffin pool retained by skin flaps.

The popliteus muscle is awkwardly placed for recording tension, its proximal tendon being within the knee joint and the distal insertion on the tibia being extended and fleshy. In some experiments, the approximate time-course of popliteus contraction was obtained by placing a force transducer in contact with the medial border of the foot, which is internally rotated along with the tibia as one result of popliteus contraction. In two experiments, the muscle's proximal tendon was severed and attached to a strain gauge (Statham Gl–80–350) so that an accurate record of tension could be obtained.

Responses of the whole PAN were recorded in continuity, with special attention being directed to the presence of tonically firing receptors with the joint held in intermediate positions. Responses of single PAN units were recorded in subdivisions of the L6 or L7 dorsal roots, or in filaments dissected from the nerve itself. Conduction velocity of the dorsal root units could be calculated from the latency of their response to electrical stimulation of the PAN, and the conduction distance measured after terminating the experiment.

In some experiments, filaments of L6 and L7 ventral roots were subdivided until only one, or in some instances more than one, antidromic action potential appeared in response to stimulation of the nerve to popliteus, at latencies characteristic of fusimotor axons (conduction velocity less than 50 m/s). The number of successfully dissected fusimotor fibres supplying popliteus spindles ranged from 5 to 22 in different experiments, and in each case they were mounted together on a pair of stimulating electrodes. No overt muscle movement during tetanic stimulation of the fusimotor bundle could be seen, although stimulation of a single large (α) motor fibre to popliteus was readily detectable. Recording and stimulation was by way of platinum electrodes and conventional recording and stimulating equipment. Instantaneous firing frequency of units could also be displayed on the oscilloscope.

Results

Afferent Discharge in Posterior Articular Nerve

In most preparations, tonic firing of a few units with impulses of large or medium amplitude was recordable from the whole PAN in continuity, with the joint held in intermediate positions (approx. 110–120° from full flexion; see Burgess and Clark, 1969). In addition, brief discharge of a number of phasic receptors could always be evoked by tapping the bone near the joint, or the joint capsule. Slowly adapting discharges in most cases could be readily augmented or reduced by small flexion-extension movements at the joint, and increased by gentle probing with a glass rod of particular regions of the posterior aspect of the joint. Especially effective in augmenting the discharge was external rotation of the tibia by passive eversion of the foot, a manoeuvre which stretches the popliteus muscle as well as distorting the joint capsule. Probing or distal displacement of portions of the popliteus muscle also accelerated the firing of some units, in agreement with the observation of Clark and Burgess (1975). In two preparations, no maintained discharge was detectable by whole nerve recording with the joint at intermediate angles, and even manipulation of the joint within this limited range failed to evoke clearcut tonic firing; responses of phasic units were, however, readily elicited.

Twitch contraction of the popliteus muscle evoked by single shock stimulation of its α motor supply, either in the nerve or in ventral roots L6 and L7, elicited a burst of discharge in the whole PAN, often with a pause in the firing of some units at the peak of contraction. Isolation of single functional units in dorsal root filaments or from the nerve itself permitted more detailed analysis. Most PAN afferent units appeared to be true phasic or tonic joint receptors, responding to probing or tapping the joint capsule, but not to outward tibial rotation. Many of these receptors were also fired by contraction of the popliteus. However, some slowly adapting PAN units showed pauses in their discharge during a twitch contraction. An example of such a unit is shown in Fig. 1, illustrating an experiment in which the proximal tendon of popliteus had been isolated and attached to a strain gauge; the lower trace thus records faithfully the time course of the twitch. Other isolated tonic PAN units showing a typical pause during contraction of popliteus were also observed, but in these the mechanical response was recorded only indirectly by monitoring the internal foot-rotation component of the muscle's action.

Occasional tonic units with properties characteristic of tendon organs were encountered. They had no resting discharge, seemed to have high mechanical thresholds and showed typical "in series" behaviour during contraction of popliteus. Fig. 2 presents an example of such behaviour, recorded from a dorsal

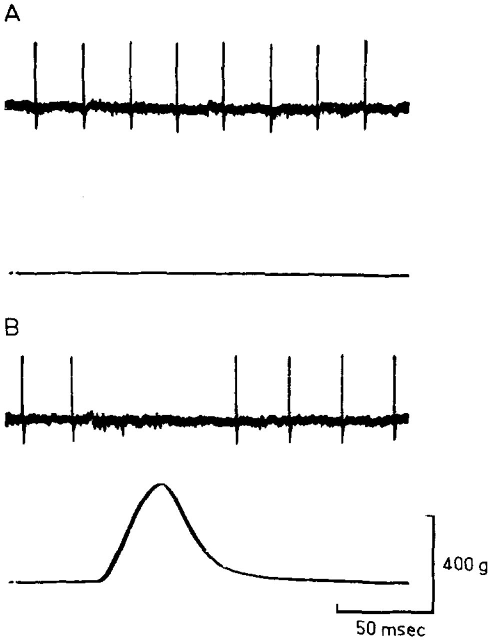

Fig. 1. Unit showing pause during popliteus twitch. A slowly adapting afferent in PAN responding in the mid-range of joint angles (110–120° from full flexion, see Burgess and Clark, 1969). **A** resting discharge; **B** interruption of discharge during twitch contraction of popliteus muscle

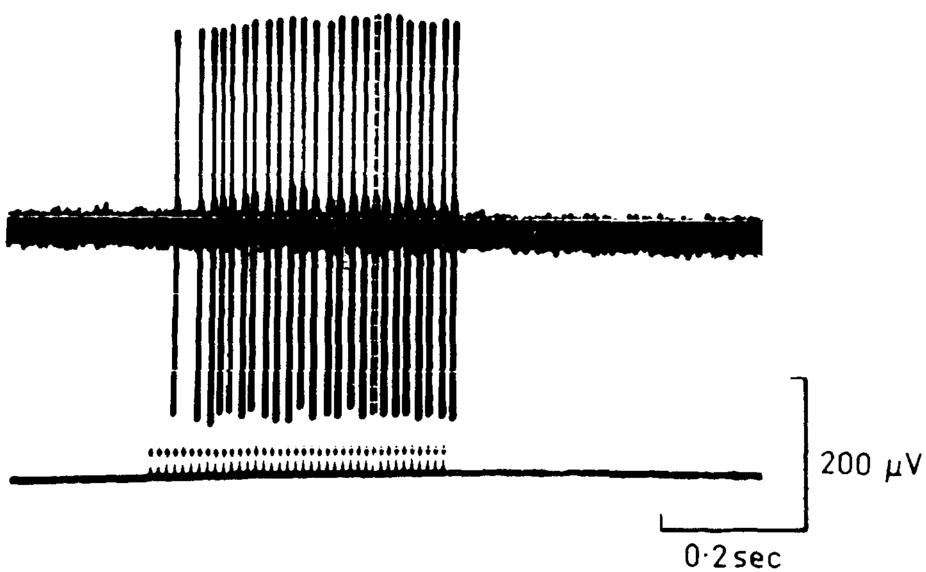

Fig. 2. Unit showing tendon organ behaviour. Slowly adapting afferent in PAN, conducting at 93 m/s. It is silent in the mid-range unless the popliteus muscle is made to contract tetanically. Stiumulation at 90 Hz for 0.4 s

root filament during a brief (0.4 s) tetanic contraction of popliteus muscle. The unit's conduction velocity was 93 m/s. There was no resting discharge, and the receptor could not be activated by mechanical probing of the joint through overlying tissue. It fired, however, in typical tendon organ fashion during tetanic contraction, beginning to respond only after the third of the 38 motor nerve volleys, and reaching peak frequency (78 Hz) after 8–10 shocks. Unfortunately, popliteus tension could not be recorded in this experiment. Whether the receptor was a typical tendon organ of popliteus, or a Golgi type ending in capsular or ligamentous tissue, (as described by Andrew, 1954), and subject to distortion by contraction of the muscle, must remain speculative.

Effects of Succinylcholine

For some of the units showing a spindle-type behaviour, the action of succinylcholine was examined. In confirmation of Burgess and Clark (1969), the resting discharge frequency of the units was increased by small intravenous doses (100–200 μg/kg) of succinylcholine chloride. Identical effects of succinylcholine were observed for popliteus spindle afferent units with their fibres running in the popliteus nerve.

Effects of Fusimotor Stimulation

In 9 experiments, filaments were dissected from the L6 and L7 ventral roots until each contained only one or two functional fusimotor (γ efferent) axons supplying the popliteus muscle, as shown by typical latency of their antidromic action potentials set up by stimulating the popliteal nerve. The ease with which these filaments could be prepared varied from preparation to preparation, and the number of fusimotor fibres available for stimulation ranged from 5–22. The effect of tetanic stimulation of the collection of fusimotor filaments, at frequencies between 100 and 330 Hz, was examined on the discharge in the whole PAN, and on single slowly adapting units dissected from the nerve or from dorsal roots. In 5 of these 9 experiments, fusimotor stimulation brought about unmistakable acceleration of discharge in the whole PAN, and of single tonically firing units isolated from dorsal roots or the nerve itself. Whole nerve recording also revealed that fusimotor stimulation could evoke firing by other units not tonically active at the joint angles used in these experiments. Fig. 3 shows a typical result of stimulating 10 fusimotor fibres of popliteus on the discharge in the whole PAN. In addition to the one firing in the absence of stimulation, several previously silent units with large spikes were strongly activated by the fusimotor volleys. Such behaviour is typical of muscle spindle receptors, and identical responses were seen in the discharge of popliteus spindle afferents which had their fibres running in orthodox fashion in the muscle nerve. Amplitudes of the action potentials recorded from the whole articular nerve indicate that they are of large diameter, and probably originate from spindle primary endings. For those units with spindle behaviour recorded

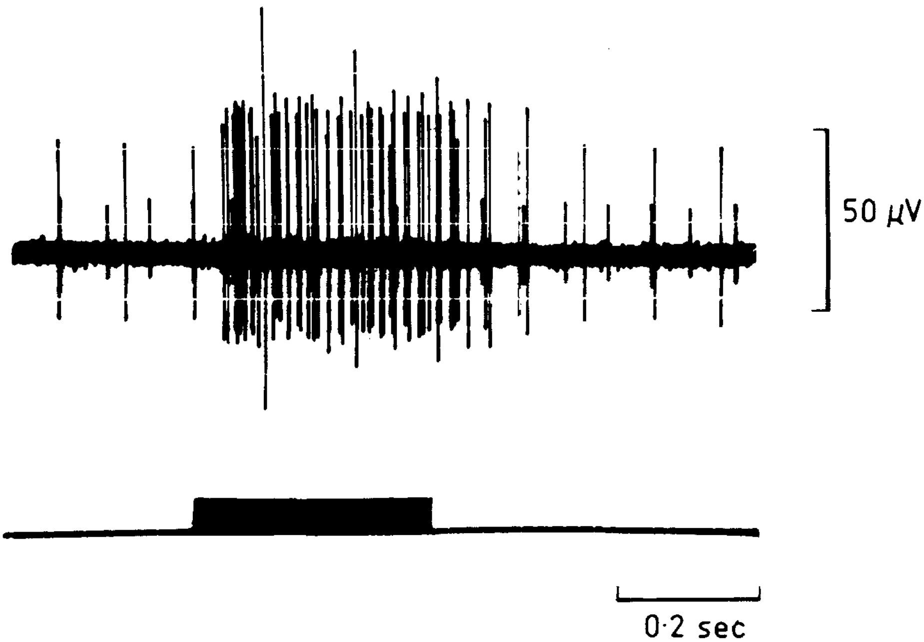

Fig. 3. Spindle units in whole PAN. Activity of afferent fibres in whole PAN is increased in response to stimulation of 10 fusimotor fibres at 330 Hz for 0.34 s. Fusimotor fibres were isolated in filaments of ventral root after being indentified as running in the popliteus nerve

from dorsal root filaments, conduction velocity measurements confirmed that they belonged to Group I. Some responses of such a unit, of conduction velocity 114 m/s, are shown in Fig. 4, the records displaying instantaneous frequency of the unit's discharge. Record A shows the large increase in discharge frequency caused by manual outward rotation of the tibia by everting the foot, and B, the smaller increase in discharge rate produced by slight extension of the knee joint with the foot slightly everted. C displays the striking increase in discharge frequency (peak 98 Hz) brought about by tetanic stimulation at 167 Hz for 2 s of 7 fusimotor fibres supplying popliteus muscle.

Discussion

Our results confirm the presence in PAN of fibres from slowly adapting endings with spindle-like properties, which respond to mechanical prodding or manipulation of popliteus, as well as knee joint manoeuvres which extend this muscle, especially outward rotation of the tibia; they also confirm the augmentation of resting discharge from these receptors by small doses of succinylcholine. Such evidence could still be regarded as equivocal, for most manoeuvres which stretch popliteus must also distort capsular and ligamentous

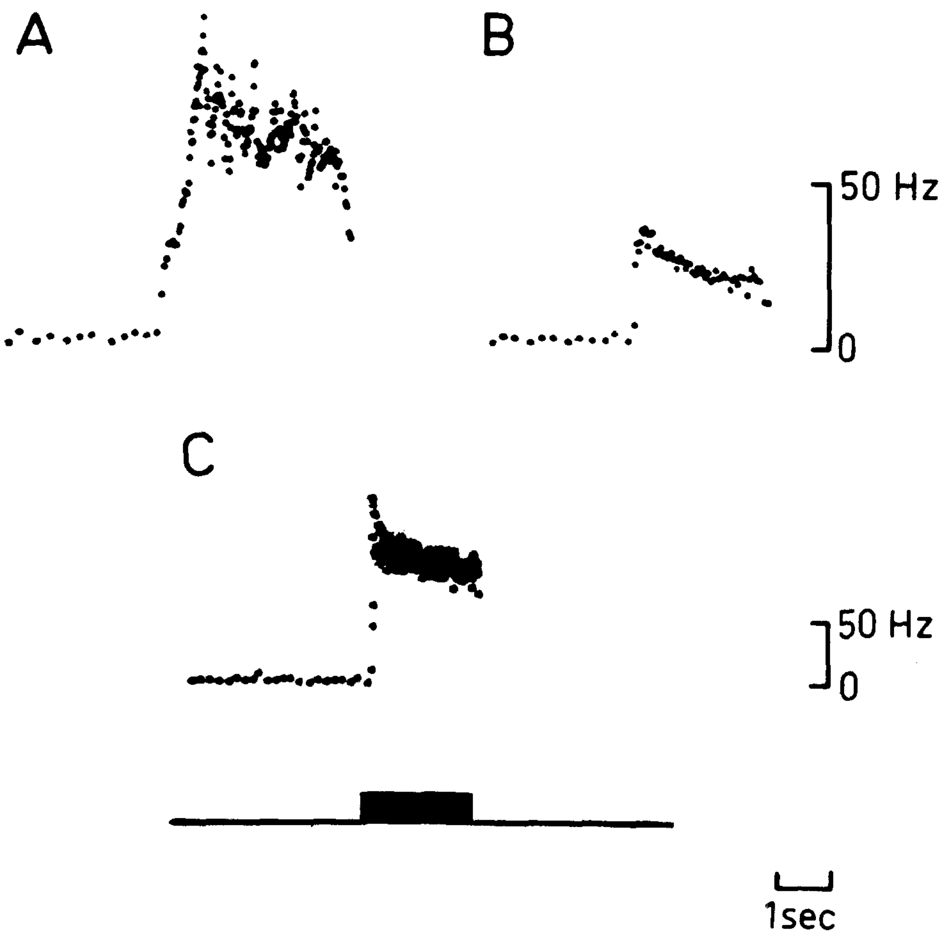

Fig. 4. Single spindle afferent. Responses of slowly adapting afferent in PAN responding to joint rotation (**A**, **B**) and fusimotor stimulation (**C**). The display of afferent firing is as an instantaneous frequency where every dot represents an action potential and the height of the dot above the baseline is proportional to the reciprocal of the interval between it and the previous action potential. **A** outward rotation of the tibia; **B** extension of the knee with foot slightly everted; **C** response to fusimotor tetanus (7 fibres stimulated at 167 Hz for 2 s). Note different frequency calibration for **A** and **B** and for **C**

structures of the joint, and because popliteus partly overlies the joint, mechanical probing from behind must often affect both joint and muscle tissue. Furthermore, the specificity of succinylcholine action has been questioned (Ferrell, 1977).

But in addition to these confirmatory findings, our experiments provide additional evidence, which we regard as definitive, that some afferent fibres in PAN which discharge tonically with the joint in intermediate positions are indeed aberrant fibres from spindles in popliteus muscle. The pause in discharge during contraction of the muscle, recordable both in the whole PAN and in single units, strongly supports this interpretation. But incontrovertible evidence for this origin is provided by the striking effect of popliteus fusimotor volleys, in the absence of any overt muscular movement during such stimulation. This augmentation of firing is typical of that evoked in spindles of other muscles, including popliteus spindles with their fibres coursing normally in the muscle nerve. An aberrant course for fibres from muscle stretch receptors has been observed in other instances, e.g., in the purely sensory crural interosseous nerve from receptors in flexor digitorum longus and flexor hallucis longus (Hunt and McIntyre, 1960; Yeo, 1976).

The regularity with which aberrant fibres from popliteus run in the PAN, and the extent of such contamination, deserves some comment, although it is likely to vary from preparation to preparation, as in the case of the interosseous nerve. In 4 of the 9 experiments in which a fusimotor bundle was available for stimulation, no effect on the PAN discharge could be detected. However, in two of these experiments, very little tonic activity was recordable from the PAN with the joint in intermediate positions, so it is possible that aberrant spindle fibres were fewer than usual or even absent in these preparations. Although 17 fusimotor fibres were available for stimulation in one of the experiments with minimal PAN tonic firing, only 8 could be isolated in the other. In the remaining 2 negative experiments with the usual extent of tonic background firing present in the PAN, in one, the L6 spinal roots were abnormal, and only 5 fusimotor axons could be isolated. A more adequate sample (22 axons) was available in the other preparation, but stimulating the bundle at 167 Hz failed to evoke augmentation of discharge. Thus it is possible that no aberrant spindle fibres were present in the PAN of this animal. Unfortunately, higher frequencies of stimulation, shown in some subsequent experiments to be necessary, were not tried in this experiment.

According to Boyd and Davey (1968), the popliteus nerve contains about 100 fusimotor axons, so the chances of the relatively few spindles with fibres in the PAN being influenced by stimulating a small sample of these axons are likely to be minimal. We consider that a bundle of 20 or more would be necessary to have a reasonable probability of activating the aberrant spindles, despite the fact that in some experiments stimulating a smaller number proved effective. It was observed in one experiment that tetanising 14 fusimotor axons had no effect, but after isolating a further 6 and adding them to the bundle, the firing of PAN tonic units was typically augmented.

In our opinion, the clearcut results of the 5 positive experiments weigh more strongly than the experiments in which no fusimotor action could be detected. We think it likely that, although aberrant spindle fibres from popliteus may be absent in some individual preparations, in the majority some afferent fibres from popliteus run in the PAN, in agreement with the conclusion of Clark and Burgess (1975).

Our experiments do not rule out the possibility that afferent fibres from secondary as well as from primary spindle endings in popliteus may also have an aberrant course in the PAN, for impulses in Group II fibres might be difficult to detect in records from the whole nerve. No special effort was made to isolate PAN units of Group II conduction velocity in dorsal root filaments; those which were studied belonged to Group I. It is also possible that some popliteus tendon organ fibres may travel by way of the PAN, e.g. the unit giving responses illustrated in Fig. 2. This unit behaved in typical tendon organ fashion, and its impulses conducted at Group I velocity. However as pointed out already, the receptor could have been a Golgi organ located in joint tissue rather than in the popliteus or its tendon.

The action of succinylcholine deserves some comment. Our experiments confirm the observation of Burgess and Clark (1969) that succinylcholine augments the resting discharge of tonic PAN units with spindle properties. However, we did not examine the effects of succinylcholine on true receptors of the knee joint, in the manner reported by Ferrell (1977). However, Burgess and Clark (1969) did not observe such an action; and recently, one of us has observed that comparable doses of succinylcholine do not elicit firing of wrist joint receptors (Tracey, 1979).

Significance for Kinaesthesia

The paucity of slowly adapting joint receptors responding to intermediate positions, as reported by Burgess and Clark (1969), Clark and Burgess (1975), Grigg and Greenspan (1977), Millar (1975) and Tracey (1979), would appear to rule out the signals from such receptors as a major factor determining position sense. However, now that it is clear that impulses from muscle spindles have access to the cerebral cortex (Oscarsson and Rosén, 1963; Landgren and Silfvenius, 1969; Phillips et al., 1971; Hore et al., 1976), they need no longer be denied an important role in position sense, whether their signals travel orthodoxly by way of the muscle nerves, or aberrantly by way of other purely afferent nerves from deep structures including joints. Furthermore, direct evidence for this is now available in man (Goodwin et al., 1972; McCloskey, 1978).

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