

The mechanoreceptor innervation of the posterior attachments of the lateral meniscus of the dog knee joint

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INTRODUCTION

Previous work in this laboratory on the structure and innervation of both dog and cat knee joint menisci has revealed that the lateral menisci consist of a central fibrocartilaginous region tethered to bone by the menisiofemoral ligament and the ligament-like horns of the meniscus. These attachments are composed of parallel bundles of collagen amongst which have been identified blood vessels, nerves and, especially in the cat, elaborate encapsulated nerve endings. The presence of these nerve endings within the ligamentous meniscal attachments has prompted the suggestion that knee joint menisci (*sensu lato*) may contribute to the sensory outflow of the joint, perhaps initiating or influencing protective or postural muscular reflexes on reaching the normal limits of motion (O'Connor, 1975; O'Connor & McConnaughey, 1978).

The present paper extends that work by presenting further evidence of the existence of an elaborate system of mechanoreceptors in the posterior attachments of the lateral menisci of dog knee joints. In addition, a mechanism is discussed by which the meniscal attachments might become increasingly taut as the knee joint moves progressively into extension (the 'close packed' position), which in turn could signal the approach of the normal limits of motion.

MATERIALS AND METHODS

Nine fresh dog knee joints were dissected in order to establish the precise anatomy of the posterior attachments of the lateral menisci. Ten additional attachments were examined histologically using a modified version of the gold chloride technique. Briefly, fresh tissues were placed in a solution of 3 parts reconstituted lemon juice (ReaLemon) to 1 part 88% formic acid, at room temperature, for 15 minutes. The tissues were then removed from the solution and placed in 1% gold chloride, in darkness and at room temperature, for 15 minutes, after which the gold chloride was decanted. The tissues were then blotted dry and placed in a 25% solution of formic acid for approximately 4½ hours. After rinsing twice in 70% ethanol, the tissues were placed in glycerol for at least 24 hours before dehydration and paraffin embedding. Serial sections, 50 µm thick, were cut and mounted on glass slides.

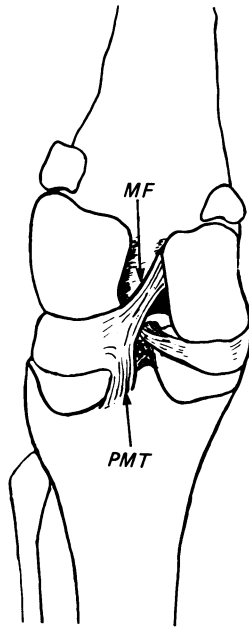


Fig. 1. Posterior view of the left knee joint of a dog illustrating the positions and attachments of the meniscofemoral (*MF*) and posterior meniscotibial (*PMT*) ligaments of the lateral meniscus.

RESULTS

Gross anatomy

The posterior attachments of the lateral meniscus of the dog knee joint were the meniscofemoral and the posterior meniscotibial ligaments. The meniscofemoral ligament was continuous with the fibrocartilaginous 'body' of the meniscus and extended medially and superiorly to attach to the lateral (non-articular) aspect of the medial femoral condyle.

The posterior meniscotibial ligament extended from the posterior and inferior aspects of the meniscofemoral ligament, and attached to the posteromedial margin of the lateral tibial plateau as it curved anteriorly to form the lateral wall of the intercondylar notch. This ligament was homologous with the posterior meniscal 'horn' in man; if the joint was dissected using a posterior approach, it was usually easily separated from the joint capsule by sharp dissection (Fig. 1).

Histology

Encapsulated nerve endings were identified in both the meniscofemoral and posterior meniscotibial ligaments. In general, those within the meniscofemoral ligament were identified within the margin that faced the inside of the joint, near the junction of the ligament with the fibrocartilaginous 'body' of the meniscus. Those identified within the posterior meniscotibial ligament were usually located near the place where it merged with the meniscofemoral ligament (Fig. 2).

To avoid confusion engendered by the use of eponyms, the encapsulated receptors and endings described in this study are referred to using the system of Freeman & Wyke (1967). At least two distinct morphotypes of mechanoreceptor were identified. In most respects these resembled Types III and II endings, previously described in

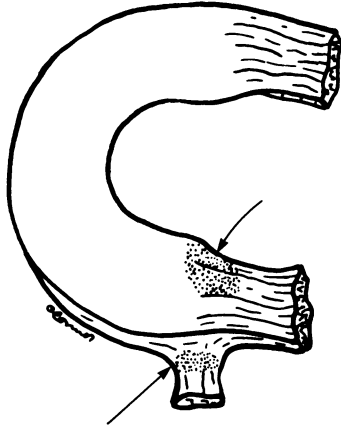


Fig. 2. Lateral meniscus from the left knee joint of a dog. The majority of the endings were identified in the stippled regions at the tips of the arrows.

periarticular tissues of the cat knee (Freeman & Wyke, 1967; O'Connor & Gonzalez, 1978).

Type III endings

Type III endings were highly variable in shape and size. Thus spherical, ovoid and stellate-shaped corpuscles were all identified. The smallest ending was spherical, with a diameter of approximately $35\ \mu\text{m}$, while the largest was ovoid, and measured approximately $50\ \mu\text{m}$ by $350\ \mu\text{m}$. Type III endings were usually served by a single myelinated axon, approximately $4\text{--}6\ \mu\text{m}$ in diameter, which pierced a thin capsule three to five laminae thick either at one pole, or at the equatorial region. Once within the capsule, the axon either lost its myelin sheath and branched immediately into a tangle of unmyelinated neurites laden with varicosities, or alternatively, the myelinated axon divided into two to six intracapsular myelinated limbs, each of which then contributed to a similar ramifying tangle of unmyelinated neurites. All unmyelinated terminal neurites either wrapped around, or lay contiguous to, intracapsular bundles of collagen which were oriented parallel to the long axis of the corpuscle, in the case of ovoid endings. In two instances collagen bundles appeared to approach from three different planes, and intersected with one another within the capsule. The capsule itself appeared to be drawn out along each of the bundles, giving the endings a three dimensional 'stellate' shape. In these receptors the neurite tangle surrounded the region of intersecting collagen. Finally, the intracapsular compartments of the Type III endings were subdivided by septa, which appeared to be derived from the inner surfaces of the capsules.

The single most complex type III ending was ovoid, and was served by at least two axons. The first axon entered the corpuscle at its equatorial region, and bifurcated at an intracapsular node of Ranvier into two terminal branches; each of the branches retained its myelin sheath and was directed towards an opposite pole of the corpuscle. Upon reaching the pole, each branch lost its myelinated sheath, changed direction, and turned back towards the equatorial region. These unmyelinated, terminal branches gave off numerous very fine varicose neurites that ramified amongst one another (Figs. 3, 4).

The second myelinated axon approached the corpuscle, lost its myelin sheath

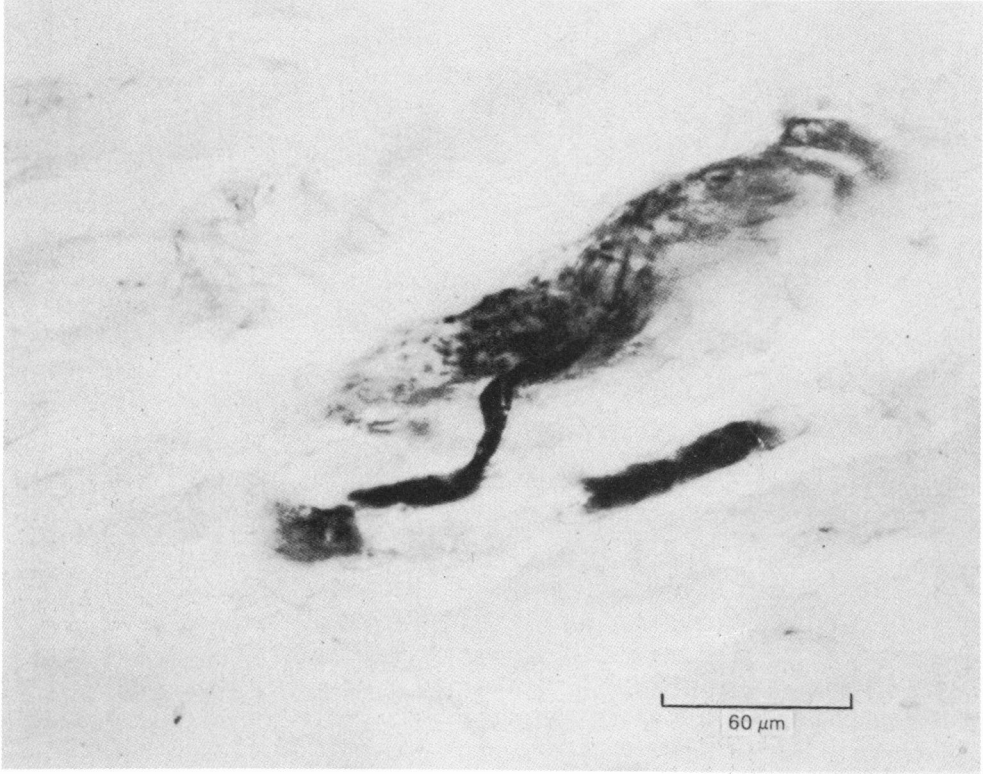


Fig. 3. Type III ending identified in the posterior meniscotibial ligament of the lateral meniscus of a dog knee joint. Gold chloride.

several hundred micrometres from the ending, and continued, as an unmyelinated neurite, to pierce the capsule midway between one pole and the equatorial region. It then became lost in the tangle of intracapsular neurites. A third unmyelinated axon was observed to leave a nearby blood vessel and to approach the corpuscle, but could not be traced into the ending with certainty (Figs. 5, 6).

Type II endings

Although paciniform by definition, at least two different forms of Type II ending were identified. The first, Type IIa, was a corpuscle of small but uniform diameter, while the second, Type IIb, was of considerably greater diameter in its proximal one quarter to one third than in the remaining distal part. As a group, Type II endings were more frequently encountered than Type III corpuscles.

Type IIa endings

The diameter of these endings seldom exceeded $60\ \mu\text{m}$, while the length ranged from approximately $200\ \mu\text{m}$ to $600\ \mu\text{m}$; the exact length was impossible to determine because the endings were exceptionally tortuous.

Although these endings were of relatively uniform diameter, their proximal portions nevertheless differed from their distal portions. Thus, each ending was served by a single myelinated axon, 4 to $8\ \mu\text{m}$ in diameter, that entered the corpuscle

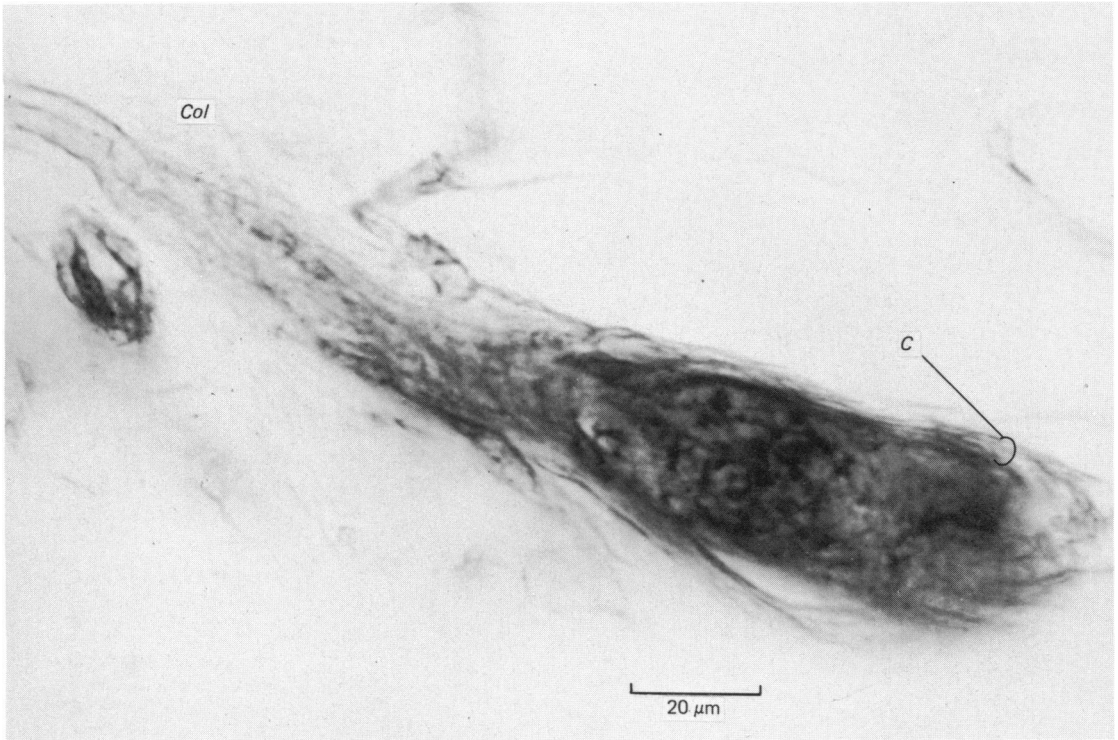


Fig. 4. Oil immersion photomicrograph of a Type III ending from the posterior meniscotibial ligament. The laminae of the capsule (C) are visible, as are two strands of collagen (Col) that have just become intracapsular. Gold chloride.

at one pole. Immediately after entry, the myelinated axon was surrounded by a subcapsular 'space' that appeared free of any stainable material. This 'space' separated the axon from the capsule, which consisted of a set of five to ten laminae about 10–20 μm thick, by a distance of 6–8 μm (Figs. 7, 8).

The distal portion of a Type IIa ending began as the axon lost its myelin sheath. At this point the unmyelinated axon became surrounded by a 'bulb' consisting of a darkly staining, granular set of concentric lamellae. These inner lamellae consisted of three to five laminae that together were 3–5 μm thick, and were enclosed by the capsule. There was usually no subcapsular space distally.

Several variations of the Type IIa endings were observed. Thus the corpuscle might bifurcate within either the proximal or distal portions. In some endings, the 'space' present in the proximal portion of an ending was continued into the distal segment, in which case it separated the inner 'bulb' from the outer capsule.

Type IIb endings

The Type IIb endings were not of uniform diameter. Rather, the proximal portion was fusiform, and its greatest diameter was approximately 130 μm . The fusiform region tapered distally, the capsule losing several laminae in the process, to a diameter of approximately 25–50 μm , at which point the distal portion of the ending began (Fig. 9). This region resembled the terminal portion of Type IIa endings in its length, tortuosity and structure.

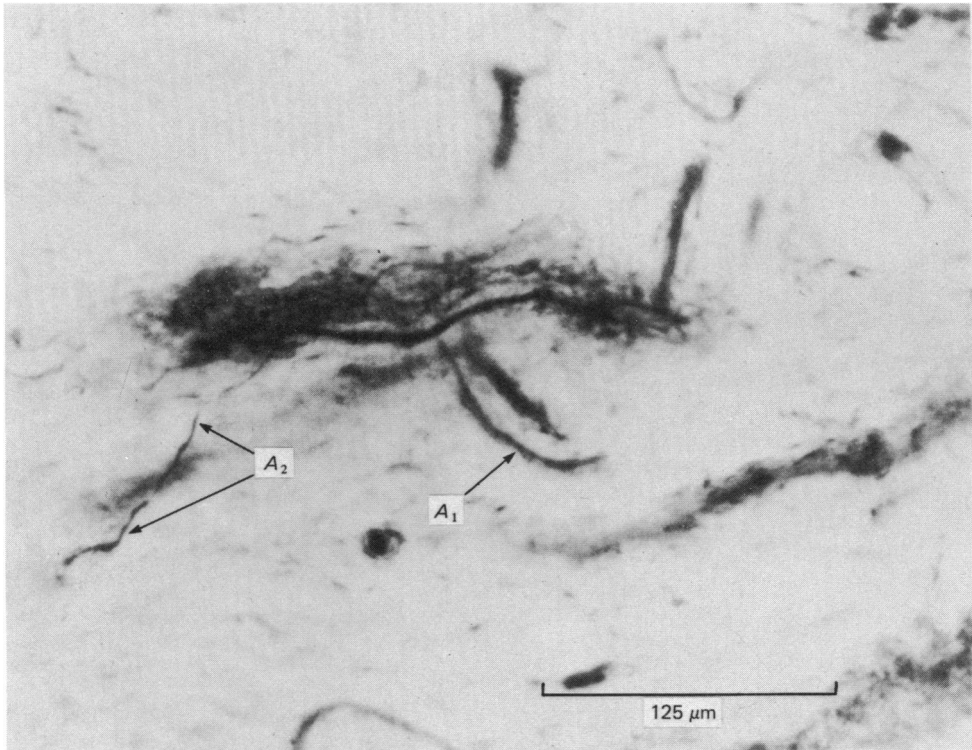


Fig. 5. The most complex Type III ending identified in this study was located in the inner margin of the meniscofemoral ligament just as it became continuous with the fibrocartilaginous meniscal 'body'. The primary axon (A_1) can be seen, as can an accessory axon (A_2), which loses its myelin sheath, and narrows abruptly just before it pierces the capsule. Gold chloride.

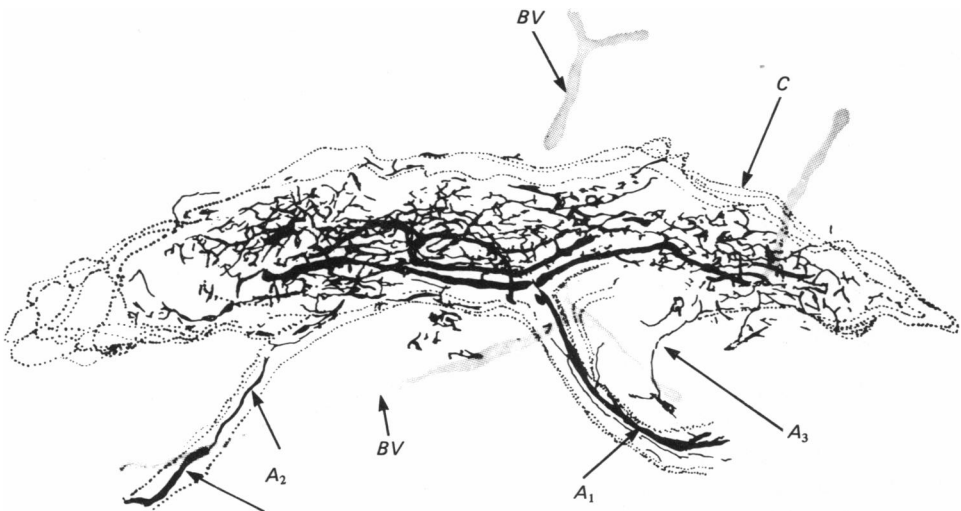


Fig. 6. Enlarged drawings of Fig. 5. This drawing was made by tracing a series of projected negatives, each of slightly different focus. The primary (A_1) and secondary (A_2) axons are illustrated, as is an additional, unmyelinated axon (A_3) that may be seen departing from a blood vessel (BV) to approach the receptor capsule (C).

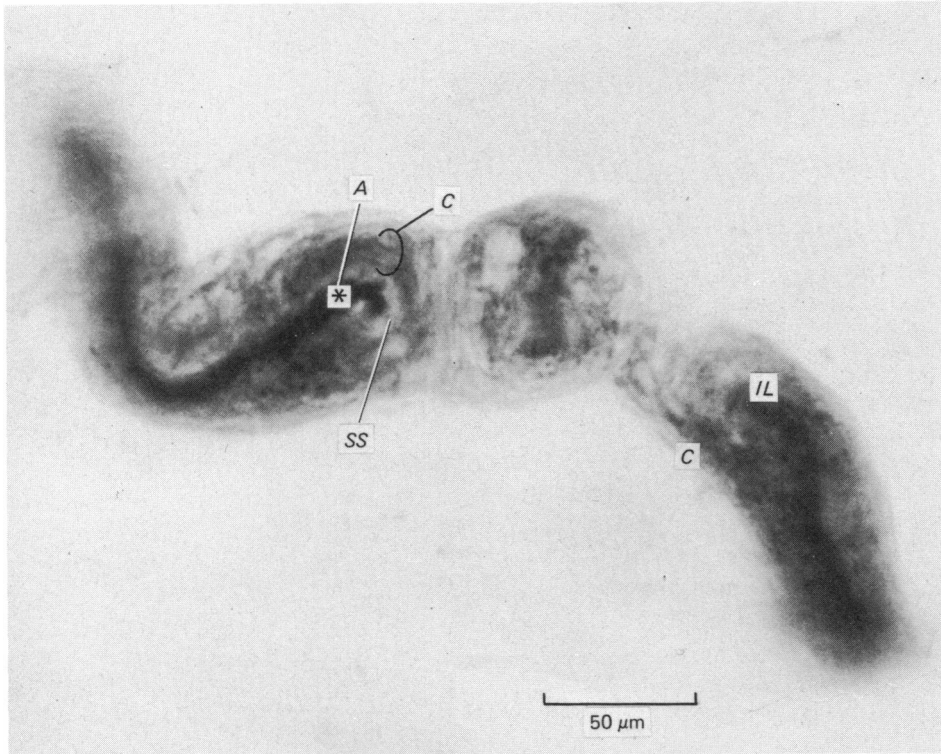


Fig. 7. Type IIa ending showing the myelinated axon (A) of the proximal region of the ending surrounded by a subcapsular 'space' (SS). The capsule (C) can be identified at both the proximal and distal regions of the ending, as can the 'bulb' of inner concentric lamellae (IL). Gold chloride.

The axons that terminated in Type IIb endings were myelinated and 5–8 μm in diameter. Typically, a myelinated axon entered the corpuscle at the proximal pole of the fusiform end, and immediately became surrounded by 10 to 15 widely spaced concentric lamellae that contributed to the corpuscle capsule. The myelinated axon continued for a distance of 125–150 μm into the corpuscle, lying within a subcapsular space, occasionally accompanied by a capillary. It then entered a 'bulb' of 5 to 10 closely spaced inner concentric lamellae and, shortly thereafter, lost its myelin sheath and continued into the distal narrow region (Figs. 9, 10).

DISCUSSION

The presence of encapsulated mechanoreceptors in the meniscofemoral and posterior meniscotibial ligaments of the lateral menisci of dog knee joints means – by definition – that the canine central nervous system is apprised of the mechanical state of the two meniscal attachments. These findings agree well with previous observations on both dog (O'Connor, 1976) and cat knee menisci (O'Connor & McConnaughey, 1978).

It is interesting to speculate on the mechanism by which these receptors could inform the central nervous system of the mechanical state of the meniscal

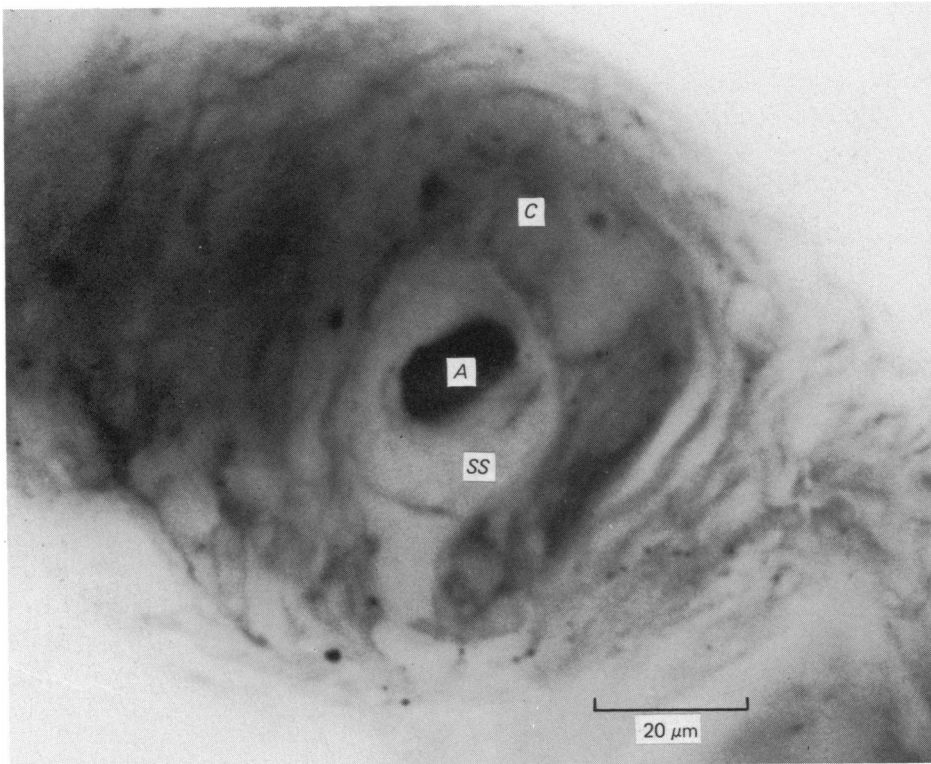
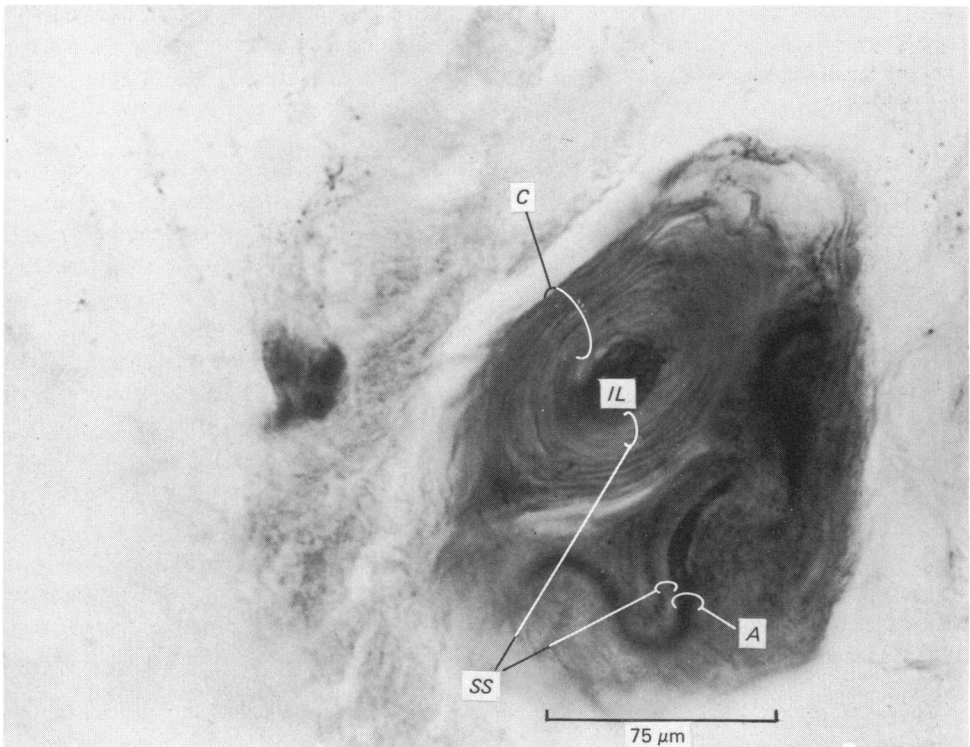
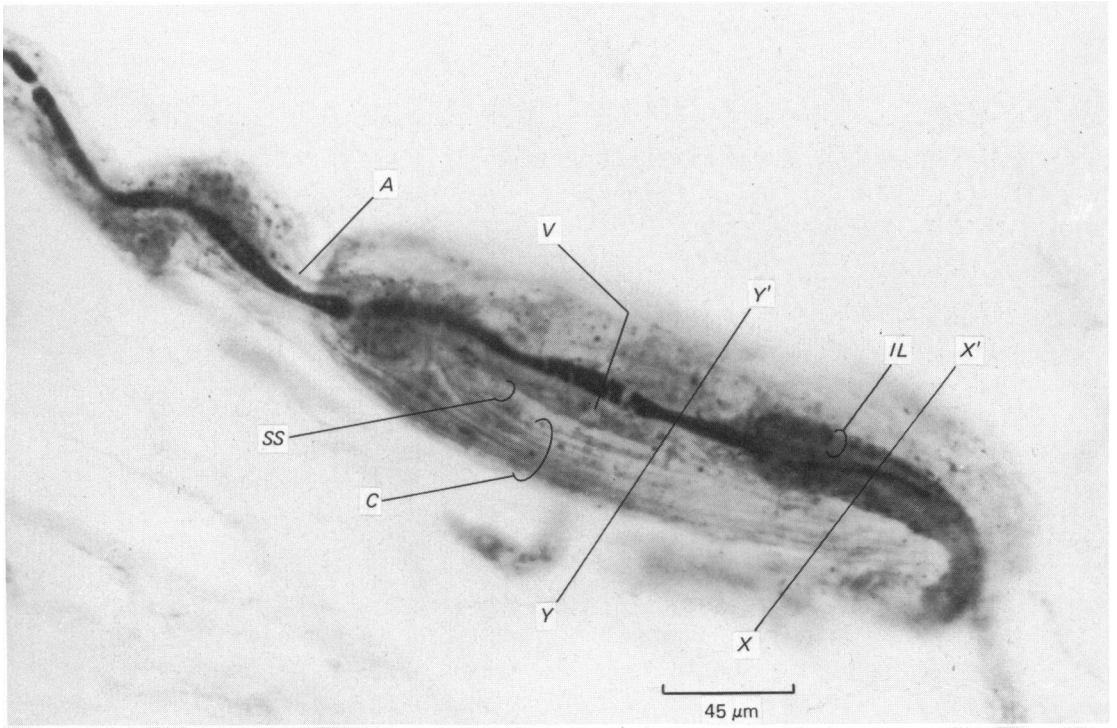


Fig. 8. Oil immersion photomicrograph of the same ending illustrated in Fig. 7, clearly showing the proximal (myelinated) axon (*A*), the capsule (*C*), and the subcapsular space (*SS*). Gold chloride.

attachments. When the knee joint is fully flexed, the posterior surfaces of the femoral condyles bear against the tibial plateaux and the superior surfaces of the menisci. In this position, it seems reasonable to suppose that the posterior meniscotibial and meniscofemoral ligaments would be lax, because the curvatures of the posterior surfaces of the femoral condyles are of relatively small radii. However, in extension (the 'close packed' position), the distal surfaces of the femoral condyles contact the tibial plateaux and the superior surfaces of the menisci. Since the curvatures of the more distal surfaces of the femoral condyles are of much greater radii, a broader surface would contact the tibial plateaux, and this would tend to force the menisci peripherally. In turn, this would place the meniscal attachments under increasing tension, and so 'trigger' the mechanoreceptors located within them.

Fig. 9. Type IIb ending showing the proximal, myelinated intracapsular segment of axon (*A*), which together with a capillary (*V*) lies in the subcapsular space (*SS*). The lamellae of the capsule (*C*) are visible, as is the 'bulb' of inner lamellae (*IL*). For *X-X'* and *Y-Y'* see Fig. 10. Gold chloride.

Fig. 10. Type IIb ending, in which the proximal region of large diameter is folded so that it is cut twice in section at location approximated by lines *X-X'* and *Y-Y'* in Fig. 9. The myelinated axon (*A*) and subcapsular space (*SS*) are visible, as are the 'bulb' (*IL*) and lamellae of the capsule (*C*). The small diameter terminal extension of the ending is not visible.



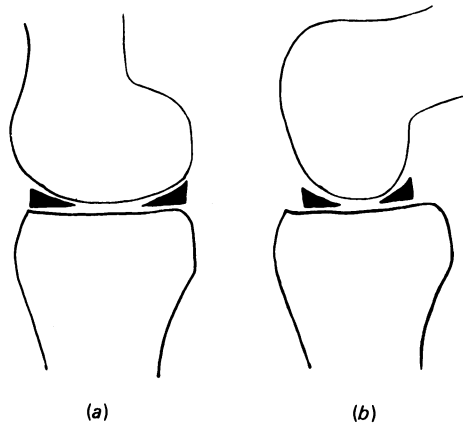


Fig. 11(a-b). When the knee joint is extended (Fig. 11a), the menisci are forced towards the periphery of the joint, thus tightening their attachments. When the knee joint is flexed (Fig. 11b), the menisci may 'recoil' inwards, thus decreasing the tension on their attachments.

Morphological affinities of Type III endings

The Type III endings described in this study closely resemble published descriptions of cat Golgi tendon organs (Merrilles, 1962; Schoultz & Swett, 1972; 1974), encapsulated endings of the cat knee joint capsule (Halata, 1977), and Type III endings of the cat medial collateral ligament (O'Connor & Gonzalez, 1979). Although these endings have different names, they appear to represent, at least structurally, but a single population. Thus, each is characterised by a thin capsule, 3-5 laminae thick, that encloses intracapsular bundles of collagen. Septa, apparently derived from the inner surfaces of the capsules, divide the intracapsular space into several compartments, and entanglements of unmyelinated neurites wrap around, or lie contiguous to the intracapsular collagen.

Extrapolating as far as possible from what is known of cat receptors, Type III receptors in the dog might be high threshold, slowly adapting endings (Freeman & Wyke, 1967; Ferrell, 1980; Skoglund, 1956; Burgess & Clark, 1969). Such endings are generally regarded as being sensitive to stretch (Rossi & Grigg, 1982), and may modulate the excitability of flexion-withdrawal and crossed-extensor reflexes (Baxendale & Ferrell, 1980, 1981, 1982), and/or serve as joint 'limit detectors' (Rossi & Grigg, 1982). These notions, of course, are consistent with earlier suggestions that knee joint menisci might serve as 'early warning' sensory devices protecting the joint from excessive motion (O'Connor & McConnaughey, 1978).

Morphological affinities of Type II receptors

Type II endings are basically paciniform, and have been referred to as Golgi-Mazzoni endings (Grigg, Hoffman & Fogarty, 1982) and Vater-Pacini corpuscles (Skoglund, 1956). Regardless of the terminology, all such endings are characterised by an axis neurite (or neurites) enclosed within a core of closely spaced 'internal' concentric lamellae, in turn surrounded by a capsule of 'outer' concentric lamellae. A subcapsular space may or may not separate the inner from the outer lamellae.

The presence of at least two forms of Type II ending (Types IIa and IIb), as well as the considerable variation within each category, raises the question of whether or not there are functional variations as well. Indeed, Burgess & Clark (1969) and

Rossi & Grigg (1982) have identified two different types of rapidly adapting discharges from receptors located in cat knee and hip joint periarticular tissues. One of these discharge patterns resembles those of Pacinian corpuscles, responding with a short duration, high frequency train of impulses to any joint movement, while the other population of rapidly adapting receptors responds only to movement along a single axis.

SUMMARY

The posterior attachments of the dog knee joint lateral menisci have been studied to identify and characterize their mechanoreceptor innervation.

Two basic types of mechanoreceptor were identified that appeared to be similar to the Type III and Type II endings described by Freeman & Wyke (1967) in cat knee periarticular tissues. Significantly, two distinct forms of Type II corpuscles were identified in this study, referred to as Types IIa and IIb, respectively.

Endings were usually identified either at the point where the posterior meniscotibial ligament merged with the main body of the meniscus and the meniscofemoral ligament, or within the inner aspect of the meniscofemoral ligament where it joined the meniscal 'body'.

The presence of encapsulated mechanoreceptors within the attachments of dog knee lateral menisci means that the central nervous system is being apprised of the mechanical state of these structures.

A mechanism is suggested by which the tension of meniscal attachments could be varied according to knee joint position.

A possible relationship between the morphology of the receptors identified in this study and the physiological responses of similar cat knee joint receptors is discussed.

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