

Segmental sensory innervation of the anterior cruciate ligament and the patellar tendon of the cat's knee

Enrique Gómez-Barrena, Enrique Martínez-Moreno and Luis Munuera

We performed a study in cats to describe and quantify the segmental sensory innervation of the anterior cruciate ligament of the knee. We also studied the patellar tendon to show that transport occurs from an extraarticular, dense connective tissue structure and to obtain comparable quantitative information. We injected a tracer (horseradish peroxidase HRP, coupled to wheat germ agglutinin WGA) in the anterior cruciate ligament and observed the reaction product in the articular nerves of the injected knee and in the cell bodies of ipsilateral dorsal root ganglia. In these experiments, we found an average of 26 (13–52) labeled neurons, mostly large, after injecting the anterior cruciate. More than half of the labeled neurons were found in the dorsal root ganglion of L7 (last lumbar segment in the cat). We counted an average of 204 (17–426) labeled neurons, mostly small, after injecting the patellar tendon. More than half of these labeled neurons were found in the L5 spinal ganglion. No product was observed in con-

tralateral spinal ganglia. Surgical ablation of the medial and lateral articular nerves (MAN and LAN) before injecting HRP-WGA in the anterior cruciate ligament, showed that the remaining afferents in the posterior articular nerve (PAN) projected mainly to L7. After excision of PAN, the projection was maintained through MAN and LAN, mostly to L5.

Our quantitative data show that the anterior cruciate ligament is poorly innervated, if compared to the patellar tendon. The anterior cruciate segmental sensory innervation is directed to L7 (corresponding to the main ventral root forming the sciatic nerve in the cat), but also to L5 and L6 (main femoral nerve ventral roots). These segmental data indicate that anterior cruciate innervation influences muscle tone regulation, not only of the hamstrings (neuromuscular system of the sciatic nerve), but also of the quadriceps muscle (neuromuscular system of the femoral nerve).

Departments of Orthopedic Surgery and Morphology, "La Paz" Hospital, Autonomous University of Madrid, Madrid, Spain. Tel +34 1-3975323. Fax -3975353. E-mail: egbarrena@mvax.fmed.uam.es
Submitted 96-03-02. Accepted 96-06-09

A sensation of instability and reduced function of the knee, after a mechanically successful anterior cruciate ligament reconstruction, may be caused by damage to the ligament's innervation (Barrett 1991).

Morphologic studies of the anterior cruciate ligament in man (Schultz et al. 1984, Schutte et al. 1987, Halata and Haus 1989, Haus and Halata 1990) and in the cat (Skoglund 1956, Freeman and Wyke 1967, Sjölander et al. 1989) described corpuscular and non-corpuscular nerve endings in the ligament as well as in the patellar tendon (Gómez-Barrena et al. 1991, 1992) and other knee structures. These mechanoreceptors initiate proprioceptive information sent to spinal ganglia through myelinic neural fibers (Freeman and Wyke 1967) via the articular nerves. Anterior (medial and lateral articular nerves, MAN and LAN) and posterior (posterior articular nerve, PAN) articular nerves can be dissected in the cat (Figure 1) and in man (Kennedy et al. 1982). Recent studies in the cat, using retrograde axonal transport

techniques from the articular nerves of the knee, showed that about 800 neurons found in the spinal ganglia were related to knee innervation (Craig et al. 1988). These data probably include sensory innervation from many articular and periarticular structures, conducted through the articular nerves.

Neurophysiologic studies showed electric activity in afferent PAN fibers of the cat's knee, during passive movements and local pressure at the proximal anterior cruciate ligament (Krauspe et al. 1992). To obtain a fast response, information from the ligaments should be redirected to muscles at the spinal level. Changes in the activity of spinal gamma-motor neurons related to periarticular muscles were observed after stretching the cruciate ligaments of the cat (Johansson et al. 1990). The sensory network in the anterior cruciate may affect the control of muscle activity around the knee, via the γ -motor neuron loop (Johansson et al. 1991). Several studies have shown muscular activity around the knee in response to high

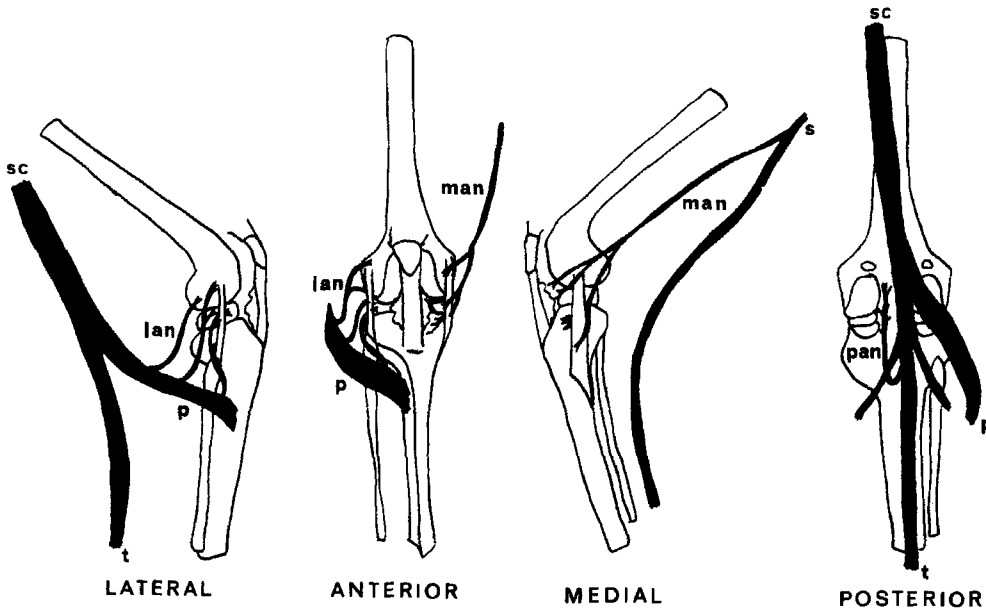


Figure 1. Schematic drawings of anterior (lateral and medial) and posterior innervation of the cat's knee. (lan lateral articular nerves, p peroneal nerve, man medial articular nerve, s saphenous nerve, sc sciatic nerve, t tibialis nerve, pan posterior articular nerve).

(Solomonow et al. 1987) and physiologic (Miyatsu et al. 1993) axial loading of the anterior cruciate ligament. These studies underline the role of proprioception in knee stability, eliciting a fast reaction of the periarticular muscles after anterior cruciate overload, while it may regulate muscle tone under physiologic loads during normal knee function.

However, we do not know precisely the anatomic pathways that would facilitate these neurophysiologic mechanisms by bringing proprioceptive information from the anterior cruciate to the spinal cord. Hilton's law, back in the 19th century, stated that nerves supplying periarticular muscles should supply joints and the overlying skin. Retrograde axonal transport techniques from the articular nerves of the cat's knee showed that labeled afferent fibers projected from L1 to S2 in the spinal cord (Craig et al. 1988). Neurophysiologic data signal that anterior cruciate traction leads to contraction of quadriceps and hamstrings (Miyatsu et al. 1993), suggesting neural pathways from the anterior cruciate to the lumbar spinal metameric levels, where femoral and sciatic nerve roots emerge. No information has been provided about the relative importance of femoral and sciatic neuromuscular systems in reacting to information from neural endings in the anterior cruciate ligament.

This study, using retrograde axonal transport techniques, was performed in the cat to obtain quantitative information about the anterior cruciate ligament neural apparatus, and to clarify its topographic seg-

mental distribution. The patellar tendon was also injected as a control of retrograde axonal transport techniques from dense connective tissue, and to provide quantitative and topographic information about neurons in spinal ganglia related to the patellar tendon.

Animals and methods

We performed the experiments in 16 adult cats weighting 3 ± 0.4 kg. We followed the recommendations of the Spanish Committee of the International Council for Laboratory Animal Science and the European Community Directive 86/809/EC to avoid animal suffering. During and after surgery, proper care was provided under the supervision of a veterinarian. Sterile surgery technique was employed after intraperitoneal injection of sodium pentobarbital (35 mg/kg), using cephazolin (100 mg/kg) as antibiotic preoperative coverage. We approached the anterior cruciate ligament of the right knee in 16 cats through a limited, anterolateral and proximal arthrotomy, sectioning the upper lateral patellar retinaculum and dislocating the patella medially; the fat pad covering the distal anterior cruciate was also displaced medially. We used this approach to avoid damage of the MAN—with a medial origin, from the saphenous nerve—, and LAN—with a lateral, distal origin, from the peroneal nerve (Figure 1). We injected 0.5–2 μ L

of a mixture of 30% horseradish peroxidase (HRP, Sigma VI, USA) and 5% HRP coupled to wheat germ agglutinin (HRP-WGA) with a Hamilton microsyringe. The microsyringe produced a precise injection of the tracer across the synovial layer (without major disruption) within the anterior cruciate ligament (special care was taken to inject a generous amount the proximal and distal ligaments where nerve endings have been observed). This tracer has been used (Mesulam 1978) to label neural somata and axons after retrograde axonal transport following injections.

In 6 cats, selective knee denervation under a surgical microscope preceded the ligament injection. In 3 of them, the anterior nerves (MAN and LAN) were excised through a medial approach to the MAN (splitting the fibers of the sartorius muscle) and a lateral approach to the LAN (through the biceps femoris). The PAN was excised through a popliteal approach in 3 animals. We planned these denervation experiments to elucidate the distribution of anterior cruciate afferents in the main articular nerves. We also intended to compare the amount of anterior cruciate ligament innervation carried by these nerves versus the whole-knee innervation, previously reported after articular nerve injection (Craig et al. 1988).

We used left knees as controls: 5 knees without injection, 2 knees with intraarticular HRP-WGA injection in the joint cavity and 3 knees with injection of the same tracer in the patellar tendon after an anterior, direct approach served as controls for the 10 injections of non-denervated right knees; 4 left knees without injection and 2 left knees with anterior cruciate ligament injection after a sham operation served as controls for the 6 injections of denervated right knees. We used controls without injection to investigate any contralateral labeling, controls with intraarticular injection to follow synovial uptake and controls with patellar tendon injection to ensure axonal transport from dense connective tissue.

On the third or fourth day after surgery, we perfused the animals under anesthesia with saline solution, followed by Karnovsky fixative with 2.5% glutaraldehyde and increasing buffered sucrose solutions. We then dissected the articular nerves and dorsal roots with their ganglia and stored them at 4°C in buffered 30% sucrose. We prepared 50 µm serial sections of the spinal ganglia. These sections followed the HRP processing technique with tetramethylbenzidine (TMB) as a chromogen, according to Mesulam (1978), and counterstaining with Nissl technique. To ensure that our injections allowed spread of the tracer to neural fibers and endings in the ligaments, these were sectioned and underwent the same

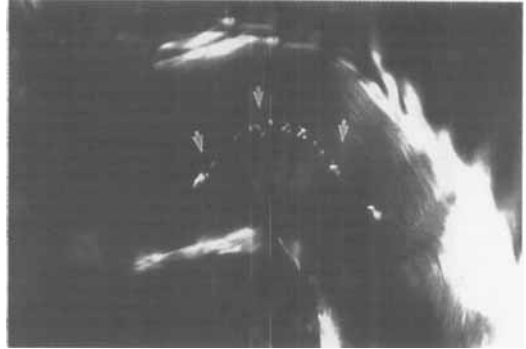


Figure 2. HRP reaction product (white arrows) in PAN fibers after ACL injection in the normal knee (darkfield under polarized light, HRP-WGA after TMB reaction; original magnification $\times 40$).

HRP processing as spinal ganglia and articular nerves. We could then observe the HRP reaction product through the ligament.

We used polarized darkfield illumination in an Axioscop Zeiss microscope (Carl Zeiss, Jena, Germany) to identify the HRP reaction product in nerve fibers (Figure 2) and dorsal root ganglia. We then plotted the distribution of the product with a camera lucida and photographed representative sections using an Ultraphot III microscope (Carl Zeiss, Jena, Germany). We considered that the neurons were labeled if they could be identified under polarized light and if under transmission light, they showed the HRP reaction product in a round or ovoid profile of a cell, as judged by the cellular nucleus (Figures 3 and 4). Quantitative data were obtained by counting every labeled neuron in every section. This was corrected for double-counting in sequential sections. We performed the statistical analysis by using Mann-Whitney and unpaired t-tests. Significance was defined as p-values below 0.05.

Results

Transport from the anterior cruciate ligament into the non-denervated knee

Retrograde axonal transport of the tracer was obtained from the anterior cruciate to the spinal ganglia cells. After performing 10 transport experiments, 4 of them were excluded: the animals had been perfused on the fourth day and most of the reaction product was outside the cells. The results of normal transport after 3 days were based on 6 experiments with a limited anterolateral surgical approach. Dissection of the articular nerves of the knee demonstrated that none of them had been damaged during surgery.

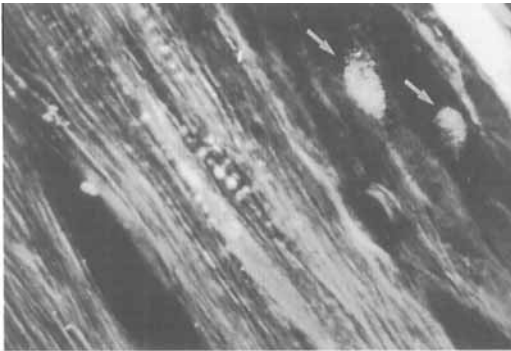


Figure 3. Labeled cells (white arrows) in L7 ganglia after ACL injection in the normal knee (darkfield under polarized light, HRP-WGA after TMB reaction; original magnification $\times 20$).

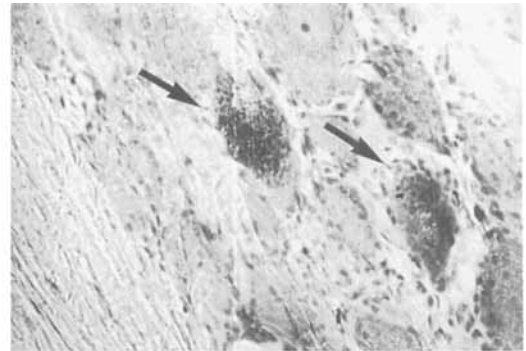
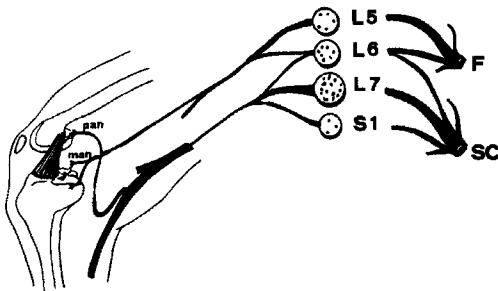
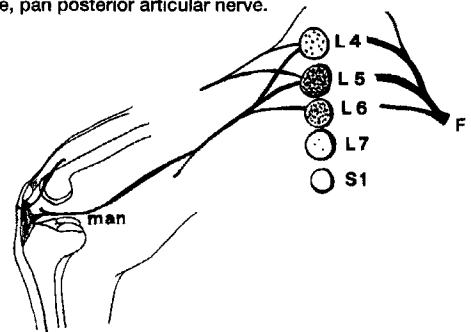


Figure 4. HRP reaction product as seen in labeled neurons (black arrows) of L7 ganglia after ACL injection in the normal knee (under transmission light, HRP-WGA after TMB reaction and Nissl stain; original magnification $\times 40$).

Figure 5. SC sciatic nerve, F femoral nerve, man medial articular nerve, pan posterior articular nerve.



A. Summary of the segmental topography of the cat's anterior cruciate ligament innervation and its correlation with lumbosacral emerging nerve roots.



B. Segmental topography of cat's patellar tendon innervation, compared to Figure 5A.

We were able to identify HRP labeling in the 3 main articular nerves of the knee. After 3 days, most of the tracer had reached the dorsal ganglia and only small amounts of the HRP-reaction product were definitely present in the MAN (3 cases out of 6) and the PAN (4 in 6) (Figure 3), but little in the LAN (1 in 6).

We also identified the HRP reaction product in the body of the ipsilateral spinal ganglion cells. No apparent clustering of labeled cells was found in the spinal ganglia. Although no preferential location of labeled cells in the ganglia was consistently observed, we identified more labeled neurons in the periphery of the most crowded ganglia, such as the last lumbar segment (L7). The involved segments were L5, L6, L7 and S1. We occasionally found some labeled neurons in L4 and S2. The average number (1 SD) of labeled ganglion cell bodies, obtained from 6 valid experiments after anterior cruciate injection in the normal knee, was 26 (16) (Table 1). Looking at the segmental distribution, means of 4.3 (5.5) labeled neurons were found in L5, 6 (6.2) in L6, 14.6 (7.5) in L7 and 1 (1.7) in S1. Correspondence with the segmental

distribution of the dissected lumbosacral plexus is shown in Figure 5A. A wide range in the number of labeled neurons was observed (1-15 neurons in L5, 1-18 in L6, 9-28 in L7 and 0-4 in S1), but L7 was always the most labeled spinal ganglion (Table 2). Measurement of labeled somata (identified in Figures

Table 1. Total number of labeled neurons after anterior cruciate ligament and patellar tendon injections in the normal and the partially denervated cat's knee

Inj.	n	Denervation	Mean	SD	Range
ACL	6	No	26	16	13-52
ACL	3	Anterior (MAN, LAN)	16*	9	9-26
ACL	3	Posterior (PAN)	11*	7	7-19
PT	3	No	204**	207	17-426

*Significant differences ($p \leq 0.05$) and **highly significant differences ($p \leq 0.01$) with labeled neurons obtained after anterior cruciate injection in the non-denervated knee. ACL anterior cruciate ligament, PT patellar tendon, MAN medial articular nerve, LAN lateral articular nerve, PAN posterior articular nerve.

Table 2. Segmental distribution of labeled neurons (from L5 to S1) after anterior cruciate ligament and patellar tendon injections in the normal and denervated cat's knee. Figures are mean (SD) range

Inj.	n	Denervation	L4	L5	L6	L7	S1
ACL	6	No		4.3 (5.5) 1–15	6 (6.2) 1–18	15 (7.5) 9–28	1 (1.7) 0–4
ACL	3	Anterior (MAN, LAN)		0 (0)* 0	0.7 (0.6) 0–1	13 (8.7) 7–23	2 (1) 1–3
ACL	3	Posterior (PAN)		5.7 (7.2) 1–14	3 (1.7) 1–4	1.3 (1.1)* 0–2	1.3 (2.3) 0–4
PT	3	No	20 (0) 20	136 (140) 7–284	56 (66) 10–133	3.3 (4.9) 0–9	0 (0) 0

*Significant differences ($p = < 0.05$) in the same segments after ACL injection in the non-denervated knee.

ACL anterior cruciate ligament, PT patellar tendon, MAN medial articular nerve, LAN lateral articular nerve, PAN posterior articular nerve.

3 and 4) showed medium-to-large diameters (20–60 μm) in 80% of the labeled ganglion cells.

In the control experiments in which one knee was not injected, we obtained no labeling in ipsilateral spinal ganglia after contralateral injection. When the tracer was injected into the joint cavity by articular puncture or arthrotomy, we could see no reaction product in ipsilateral ganglia. In 3 experiments, we injected the tracer into the patellar tendon through an anterior, direct approach and we obtained an HRP reaction product in the lumbar spinal ganglia. Labeled neurons after patellar tendon injection (mean 204 (207), with a range of 17–426 labeled neurons) showed a seven-fold increase ($p = < 0.01$), as compared to labeled neurons after anterior cruciate injection. The diameter of these labeled neurons was smaller (sampled—one in every three sections—and measured: 90 % between 10 and 40 μm), with a few large cells. The segmental distribution transport from the patellar tendon included labeling of L3 (2 (0)), L4 (20 (0)), L5 (136 (140)), L6 (58 (66)) and L7 (3.3 (4.9)). Correspondence to the segmental distribution of the lumbar plexus is shown in Figure 5B. The dorsal root ganglion of L5 represents about two thirds and that of L6 represents about one fourth of the whole innervation from the patellar tendon, as shown by transport experiments.

Transport from the anterior cruciate ligament into the partially denervated knee

We were able to identify the HRP reaction product in spinal ganglia cells after partial denervation of the knee. There was a general decrease in the number of labeled neurons following anterior cruciate injection after excision of the MAN and LAN (15.7 (9.1) neurons were labeled in these experiments) or the PAN (with 11.3 (6.7) labeled neurons) (Table 1). This decrease was significant ($p \leq 0.05$).

As compared to anterior cruciate injections in the non-denervated knee, excision of the MAN and LAN prior to injection produced a decrease in the number of labeled cells in the rostral segmental ganglia (L5

and L6) (Table 2). The differences were found to be significant for L5 ($p < 0.05$). In contrast, the number of L7 labeled cells showed no significant change (Table 2). S1 labeling was not apparently affected by the MAN and LAN excision, suggesting that the PAN can carry the tracer towards S1, but too little of the product was present to allow any precision.

Compared to anterior cruciate injections in the non-denervated knee, excision of the PAN prior to injection produced a decrease ($p = < 0.05$) in the number of L7 labeled cells (1.3 (1.1)). Instead, L5 labeling remained unmodified (5.7 (7.2)). Therefore, PAN conducts half of the anterior cruciate ligament sensory information to L7 neurons, and some to L6 and S1 neurons. Anterior articular nerves (MAN and LAN) drive some anterior cruciate sensory input towards L5, L6, and S1 (Figure 5A).

The diameter distribution of labeled cells remained unchanged after anterior denervation. Large labeled neurons at L7 were rare after posterior denervation.

Discussion

Morphologic and neurophysiologic studies concerning knee innervation have been classically performed in the cat's knee. The cat's knee has 3 main articular nerves (MAN, LAN and PAN) (Freeman and Wyke 1967), as shown in Figure 1, and 7 lumbar segments. Considering the anatomy of the cat's lumbosacral plexus and spinal ganglia, a parallelism can be shown between man and cat (Table 3) for experimental purposes, and the last lumbar segment (L5 in man and L7 in the cat) can be considered as a reference.

Table 3. Comparison of lumbosacral roots and nerve trunks of the lower limb in man and in the cat

	Femoral nerve	Obturator nerve	Sciatic nerve
Cat	L4 L5 L6	(L4) L5 L6	L5 L6 L7 S1 (S2)
Man	L2 L3 L4	L2 L3 L4	L4 L5 S1 S2 S3

Axonal transport experiments on the cat's knee have been performed by injections of the main articular nerves (Craig et al. 1988). We developed our model of anterior cruciate ligament and patellar tendon injections to obtain more precise information. Several criticisms can be raised against our injections. Dense connective tissue may compromise the neural uptake of the tracer. Secondly, synovial uptake of the tracer may jeopardize the results. Thirdly, contralateral injections labeling ipsilateral neurons would imply crossed pathways through the spinal cord that would affect our interpretation. To answer the first criticism, the patellar tendon was also injected. Retrograde axonal transport after injection indicates the possibility of obtaining HRP-WGA transport from neural fibers and endings in dense connective tissue. No intraarticular transport could be invoked after patellar tendon injections. To check further the tracer distribution in dense connective tissue, sections of the injected ligaments were obtained and the reaction showed a large spread of the product across the whole ligament. In reply to the second criticism, control experiments injecting the same amount of tracer intraarticularly showed no transport to spinal ganglia. This fact may simply mean that more tracer is needed to obtain enough synovial uptake to produce a detectable transport. It nevertheless proves that a small amount of tracer accidentally dropped into the joint would not interfere with ligament injections, because of synovial uptake. Thirdly, we obtained no labeling in ipsilateral spinal ganglia after contralateral injection. All these control experiments indicate the high specificity of our technique. Spinal cords were studied for transganglionic transport, which was rare. To increase this transport, more extensive injections would be required, increasing the risk of overestimation of anterior cruciate transport. Spinal cord data were not considered in the results. Regarding the partial denervation technique, we performed excision of the MAN and LAN in the same experiments, since both nerves are thought to innervate the distal anterior cruciate and the anterior knee. Due to variability, smallness and relative unimportance of the LAN, it was not considered independently, but rather as an additional disturbing factor in distal anterior cruciate innervation. No previous transport experiments or significant mention has been made regarding LAN's role in anterior cruciate innervation. Our findings may suggest that some of the anterior, distal innervation may be directed through the LAN, although to a minor extent. Excision of the PAN through a popliteal approach was performed, with careful manipulation of popliteal vessels and nerves to avoid local complications.

References to quantitative neural tissue in the ante-

rior cruciate ligament are imprecise. Initial reports on human ligaments (Schultz et al. 1984) found only 1–3 neural endings per ligament. Later gold-chloride histological studies (Schutte et al. 1987) claimed to observe 1% of stained neural tissue in human ACL, although the images provided showed only confusing, darkly stained structures, where neural endings could not be distinguished from vessels, as other authors have already pointed out (DeAvila et al. 1989). Thus, this quantification is controversial. Histological and electron microscopic studies helped other authors (Halata and Haus 1989, Haus and Halata 1990) to confirm 26 mechanoreceptors in human anterior cruciate ligaments, although no data on receptor variability per ligament were provided. Immunohistochemical staining or other techniques sampling thin sections (usually 5–10 μm) of the ligament could hardly provide more accurate data for estimating the number of the huge corpuscular neural endings (with a size up to 100–400 μm) in the ligaments. Quantification of total neural tissue in the anterior cruciate ligament remains controversial. Retrograde axonal transport techniques provide specific information of quantitative well-functioning innervation (with sustained pyknotic uptake and axonal transport of the tracer, both required in these experiments (Kristensson 1970, Lavail and Lavail 1972, Brodal 1981)). These techniques also provide an estimate of the fiber diameter (related to neuron size (Craig et al. 1988, Heppelmann et al. 1988)). Finally, specific data on segmental distribution of afferents in spinal ganglia (McLachlan and Jänig 1983) can be obtained. Regarding quantitative data provided by our study, there is a potential risk of overestimating the number of anterior cruciate-related neurons, although the need for a pyknotic, active uptake in neural structures reduces this possibility. The second source of overestimation could be a synovial uptake from the joint, which was not obtained in control experiments. There is also a risk of underestimating the number of related cells, due to injection of a small amount or misplacement of the tracer in the ligament. This was avoided by generous injections in different locations of the ligament, and was further assessed through sections of the whole ligament and subsequent processing which confirmed that the reaction product had spread through the whole ligament. Moreover, underestimation can follow inadvertent surgical damage of articular nerves (which was avoided in surgical approaches and controlled in necropsies). Finally, underestimates can occur after allowing a long time for transport, the tracer leaving the spinal ganglia cells. We observed that 3 days' transport experiments showed that most of the product in the cells was outside the cells after 4 days. Therefore,

we considered only the experiments with 3 days of transport.

Our data show that the anterior cruciate ligament has poor innervation compared to the patellar tendon (1/7, in this study) or with the whole knee (1/30, Craig et al. 1988). However, variability proved to be considerable. A biological or a technical effect? All the experiments showed retrograde axonal transport, with the same pattern of distribution. Free endings and amyelinic fibers may be highly variable and are usually not estimated in most reports, although always mentioned (Gardner 1948, Freeman and Wyke 1967, Kennedy et al. 1982, Schultz et al. 1984, Schutte et al. 1987, Sjölander et al. 1989). This fact may cause some variability. Histologic quantitative data also show considerable variability: from 1 to 3 endings (Schultz et al. 1984) to 26 endings (Haus and Halata 1990). This last histologic reference to neural endings in the human anterior cruciate ligament parallels our average finding in the cat (26 labeled neurons). Differences have been observed in the complexity of neural endings (Polacek 1965) among species, without mentioning significant number variability. Another morphological feature under study was the neuronal size, since its categories relate to fiber diameter (Davenport and Ranson 1931, Heppelmann et al. 1988). A higher incidence of medium-to-large labeled ganglion cells was observed after anterior cruciate injection of the tracer, suggesting a transport via myelinated fibers which would be explained by corpuscular ending tracer uptake. The fact that this ligament innervation could be mostly related to corpuscular endings, following thick, myelinic fibers onto big neurons, suggests a lesser but probably more precise amount of information about the anterior cruciate ligament. Injections of the patellar tendon produced more than 200 labeled neurons (two fifths of the anterior sensory innervation of the knee obtained in MAN injections (Craig et al. 1988)). Most neurons with a small diameter suggest amyelinic fibers—namely, free nerve endings (carrying pain information) or vascular sympathetic fibers. The rarity of big neurons suggests that little proprioceptive information is obtained at the patellar tendon, if compared with information about pain.

Our findings provide morphological evidence about the segmental distribution of the information obtained at the anterior cruciate ligament. This is sent to the originating segments of the sciatic nerve (L6 to S2) and the femoral nerve (L3 to L6), via the posterior, medial and lateral articular nerves, as observed in Figure 5A. The information from the patellar tendon, mainly via the MAN, reaches the originating segments of the femoral nerve (L3 to L6), as observed in

Figure 5B. Selective surgical denervation shows that transport from the anterior cruciate ligament significantly decreases after articular nerve excision. This conclusion stands whether anterior or posterior nerves are excised, indicating that both anterior and posterior articular nerves carry information from the anterior cruciate ligament. The remaining innervation after PAN excisions (mainly through MAN) is mostly directed to L5 (related to the originating roots of the femoral nerve). The remaining innervation after the MAN and LAN excisions (directed through the remaining PAN) mostly reaches L7 (related to the sciatic nerve in the cat). Biomechanical (O'Connor 1993) and neurophysiological data (Solomonow et al. 1987) provide evidence of a significant reaction of the hamstrings to anterior cruciate loading. Recently, quadriceps reaction to anterior cruciate loading has been identified (Miyatsu et al. 1993). Our data provide morphological support for this quadriceps reaction, based on segmental coincidence and supported by the existence of segmental pathways through a γ -motor neuron loop (Johansson et al. 1991). In the balance between hamstrings (sciatic nerve system) and quadriceps (femoral nerve system), regulated by additional information from the knee joint, proprioception obtained at the anterior cruciate ligament may contribute substantially.

Acknowledgements

Financial support by D.G.I.C.YT. (Dirección General de Investigación Científica y Técnica) grant PM88-0054, Spain.

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