

Current Concepts Review

Mechanoreceptors in Joint Function*

BY TOM HOGERVORST, M.D.†, AMSTERDAM, THE NETHERLANDS, AND RICHARD A. BRAND, M.D.‡, IOWA CITY, IOWA

Most surgeons and investigators consider ligaments to be passive stabilizers of the joints. However, more than 100 years ago, clinicians and investigators recognized the presence and potential roles of mechanoreceptors in the function of joints^{32,93,138}. Perhaps because of the frequency of injuries of the anterior cruciate ligament, the functional impairment resulting from them, and the issue of whether the anterior cruciate ligament should be removed during total knee replacement, the role of mechanoreceptors in the anterior cruciate ligament recently has attracted considerable attention.

It is important to ascertain the role of mechanoreceptors in the function of intra-articular ligaments in order to determine the future direction of joint reconstruction. Their importance, or lack thereof, will determine, in part, whether efforts should be directed more toward preservation of the receptors or whether the emphasis should remain on purely mechanical and kinematic aspects of joint function.

Joint mechanoreceptors have been most often studied in the knee, with most recent investigations focusing on the anterior cruciate ligament. In exploring the function of mechanoreceptors in the knee, we do not intend to imply that mechanoreceptors in other joints are not important; our review is merely reflecting the literature relating to loss of function of the anterior cruciate ligament due to rupture (injury) or transection (operative treatment) rather than congenital laxity.

The presence of mechanoreceptors in the anterior cruciate ligament^{41,66,104} has led several authors to suppose that these receptors influence motor function and, conversely, that their loss leads to dysfunction^{11,40,81}. This notion is reinforced by the lack of a clear association between the functional outcome and the amount of passive laxity, not only after non-operative treatment^{23,38,118,142} of tears of the anterior cruciate ligament but also after reconstruction or repair^{14,20,70,92,145,160}.

Loss of the anterior cruciate ligament alters the kinematics of the knee¹¹⁴ and probably induces a change in the stimulation and the afferent signals or output of

the remaining mechanoreceptors — for example, those in the joint capsule^{55,86}. Therefore, the function of the receptors of the anterior cruciate ligament *per se* must be distinguished from that of the remaining receptors in the knee. In view of the large number^{31,96} and substantial sensitivity of periarticular receptors^{59,60,62}, an experimental design that explicitly excludes the effects of the remaining receptors is critical for determining the function and importance of the receptors of the anterior cruciate ligament alone.

In this article, evidence that mechanoreceptors may have an effect on neuromuscular function is presented; clinical issues (proprioception, muscle reflexes initiated by the mechanoreceptors of the anterior cruciate ligament, muscle stiffness, quadriceps-force deficits, gait analysis, and electromyographic changes) are discussed; and the relationship between basic (animal) research and the clinical aspects of injuries of the ligament is considered.

Anatomical Studies

The terminology that has been used in discussing mechanoreceptors has varied among authors. Freeman and Wyke⁴¹ synthesized a number of previous reports and condensed this terminology into four types (Table I). Many but not all authors use their terminology, and so will we, except when it is not appropriate.

Relative Scarcity of Mechanoreceptors in the Anterior Cruciate Ligament

Neurotracer studies have indicated that each ligament in a cat contains a total of six to twenty mechanoreceptors¹⁰⁴ or, including free nerve-endings, thirteen to fifty-two⁵³ (Table II). There also are very few receptors in humans; monoclonal antibody stains demonstrated a maximum of seventeen mechanoreceptors in the anterior cruciate ligament of a three-year-old child⁹⁵ (Table III). These numbers decrease with age and disease^{133,146}. Placed in perspective with the innervation of the entire knee joint (as reflected by the total number of afferent nerve fibers), the receptors in the anterior cruciate ligament constitute a small minority (Tables IV and V). Comparable quantitative data are lacking for other ligaments and joints, although mechanoreceptors and free nerve-endings have been found in virtually every joint that has been studied (Tables VI and VII). The scarcity of receptors has been used to argue that they have mi-

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†Department of Orthopaedic Surgery, OLVG Hospital, P.O. Box 95500, 1091 HM Amsterdam, The Netherlands.

‡Department of Orthopaedic Surgery, University of Iowa Hospitals and Clinics, 2430 Steindler Building, Iowa City, Iowa 52242-1008.

TABLE I
CLASSIFICATION OF JOINT MECHANORECEPTORS*

Type	Morphology	Average Size (μm)	Location	Diameter of Afferent Fibers (μm)	Eponyms Used by Other Authors
I	Globular or ovoid corpuscle with thin capsule	100 x 40	Joint capsule, periosteum, ligaments, tendons	5-8	Ruffini, Golgi-Mazzoni
II	Cylindrical or conical corpuscle with thick, lamellated capsule	280 x 120	Joint capsule	8-12	Pacini, Krause, Vater-Pacini
III	Fusiform corpuscle with thin capsule	600 x 100	Ligaments, tendons	13-17	Golgi, Golgi-Mazzoni
IV	Unmyelinated free nerve-endings	0.5-1.5	Joint capsule, periosteum, ligaments, tendons, blood vessels	0.5-5	Not reported

*Modified from the system of Freeman and Wyke⁴¹.

nor importance. However, there is no *a priori* reason to believe that small numbers of receptors cannot serve important functions.

Most receptors have been reported to be located in the subsynovial layer and near the insertions of the anterior cruciate ligament (Tables II and III). The synovial tissue that enfolds the anterior cruciate ligament consists of an intimal layer facing the joint cavity and a subsynovial layer, in direct contact with the anterior cruciate ligament, containing neurovascular structures. The posterior articular nerve is the major nerve for the anterior cruciate ligament, although afferent fibers have also been demonstrated in the medial and lateral articular nerves⁵⁴.

Ruffini Receptors and Free Nerve-Endings

The receptors in the anterior cruciate ligament are primarily Ruffini receptors and free nerve-endings. Ruffini receptors are the most frequently described mechanoreceptors; Pacini receptors are reported less commonly (Tables II and III). Ruffini receptors are thought to function as stretch receptors^{59,60,74,109}, while Pacini receptors seem to be activated mainly by compression^{24,62}. Ruffini receptors have a variable morphology and are classified on the basis of electromicroscopic images^{65,68}. The Ruffini receptors of the subsynovial layer of the anterior cruciate ligament are ovoid in shape and measure approximately fifty by 500 micrometers. They are composed of nerve-endings, endoneural connective tissue, and an incomplete perineural capsule. The endoneural connective tissue consists of collagen fibrils and fibroblasts and is connected to the surrounding tissue through gaps in the perineural capsule⁶⁶. In ligaments with parallel-oriented fibrils, the perineural capsule is well developed and the Ruffini corpuscles resemble Golgi tendon organs^{65,68}. Pacini receptors have an oval shape; measure approximately 150 by 600 micrometers; and have a thick, lamellated capsule, which consists of fifteen to thirty layers of flat perineural cells. The single afferent fiber, which measures four to eight microme-

ters, divides inside the capsule into several branches, which then lose their myelin sheath. The nerve terminals are filled with mitochondria and clear vesicles with a diameter of twenty nanometers and with unknown contents⁶⁶.

While investigators have reported many different classes of receptors in many ligaments (Tables II, III, VI, and VII), these classification systems have been called into question because of several fundamental problems. First, there is controversy about the classification of individual receptors; some authors have suggested that these receptors are not distinct types but rather represent a continuum perhaps related to the adaptation of given receptors to local conditions^{5,22,65}. Second, traditional gold and silver-chloride stains are non-specific and stain vascular and other structures containing collagen and elastin^{42,130}; serial sections are essential for proper interpretation. When such sections have not been obtained, the results of a study are open to question as what appears to be a mechanoreceptor on one or two sections may in fact be a vascular structure^{32,66,89,102}. Third, classification alone does not imply function. Given these and other problems, when inferring function an investigator must interpret studies of types and numbers of receptors with considerable caution.

Free nerve-endings are more numerous than mechanoreceptors and function as nociceptors. They react to inflammation of the joint and pain stimuli, but they also function as high-threshold mechanoreceptors^{25,72,135-137}. In addition, vasoactive neuropeptides such as substance-P and calcitonin gene-related peptide have been reported in 10 per cent (2731 of 27,624) and 33 per cent (373 of 1123) of afferent free nerve-endings^{69,134}. Both of these neuropeptides are found in the cell bodies of the dorsal-root ganglion and their sensory afferent fibers, and both are thought to be involved in the processing of nociceptive information, but they also behave as vasoactive substances⁵⁰. Thus, afferent free nerve-endings in joints not only transfer information but also serve a local effector function⁷⁵ by releasing neuropeptides.

TABLE II
MECHANORECEPTORS IN THE ANTERIOR CRUCIATE LIGAMENT OF CATS

Authors, Method	Types of Receptors	Size of Receptors (μm)	Total No. of Receptors	Location of Receptors \dagger in Ligament	Diameter of Afferent Fibers (μm)
Boyd ²² (1954)*; non-serial gold-chloride sections	1 type: Golgi tendon organs	500 \times 125	2	Near capsule	12
Skoglund ⁴¹ (1956); non-serial gold-chloride sections	1 type: Golgi tendon organs	800 \times 300	Not reported	On surface	10-15
Freeman and Wyke ⁴¹ (1967); serial silver and gold-chloride sections (insertions not studied?)	2 types: Type III, Golgi-like	100 \times 600	"Several"	Close to both insertions	14-16
	Type IV, free nerve-endings	0.5-1.5	"Large numbers"	Mostly superficial	1-5
Sjolander et al. ¹⁴⁰ (1989); 20- μm longitudinal serial gold-chloride sections, including insertions	4 types: Golgi-like Ruffini Pacini Free nerve-endings	Not reported	Not reported	Subsynovial or close to insertions	Not reported
Koch et al. ⁸⁹ (1995); 70- μm longitudinal serial gold-chloride sections, including insertions	2 types (Freeman and Wyke ⁴¹): Type III, Golgi-like	100 \times 600	1-3	Mid-substance	Not reported
	Free nerve-endings	Not reported	Not reported	Not reported	Not reported
Gómez-Barrena et al. ⁵³ (1996); 50- μm serial wheat-germ agglutinin-horseradish peroxidase sections of spinal ganglia (retrograde tracer study)	Not applicable	Not applicable	13-52 labeled neurons in spinal ganglia	Not applicable	Not reported
Madey et al. ¹⁰⁴ (1997); 20-50- μm longitudinal serial wheat-germ agglutinin-horseradish peroxidase sections (anterograde tracer study)	2 types: Ovoid ending	100	5-17	"Along entire length of ligament"	Not reported
	Large ending	1000-1500	1-3	"In body of each ligament"	Not reported

*The insertions were not studied. The posterior joint capsule was studied, with observation of posterior-cruciate-ligament receptors an incidental finding: "In one case the [capsule] specimen included part of one of the cruciate ligaments, and this contained typical tendon organs of Golgi."

This local effector function can take the form of diverse possible actions of the free nerve-endings, including vasodilation, an increase in venular permeability, trophic effects, and effects on the immune system⁷⁵. Free nerve-endings therefore may have a modulatory function in normal tissue homeostasis or in the remodeling of grafts.

Lack of Regeneration of Mechanoreceptors

Mechanoreceptors probably do not regenerate, despite the fact that several reports have suggested that reinnervation with mechanoreceptors occurs after reconstruction of the anterior cruciate ligament^{13,35}. Goertzen et al.⁵¹ reported ingrowth of mechanoreceptors into allografts, but that paper has since been withdrawn⁴⁸. Confirmation of regeneration of mechanoreceptors in conventional histological studies is difficult. Histological examination of the graft material as a control before implantation is needed. Furthermore, the viability

and function of the structures that are being reported on ideally should be verified. Verification of the former is possible with use of immunohistochemical methods. In one study in which such methods were used, nerves containing substance-P and calcitonin gene-related peptide were identified in remodeling patellar ligament autogenous grafts in rats⁶. However, biopsy specimens of patellar ligament autogenous grafts obtained from humans five to thirty-seven months postoperatively showed no neuropeptide immunoreactivity.

A modulatory function of sensory innervation during graft-healing has been hypothesized⁸. This function may be comparable with the role of neuropeptides in fracture-healing^{76,116} and myocutaneous flaps^{67,91}. It seems likely that neovascularization is accompanied by ingrowth of neural structures with a neurosecretory paracrine function.

Although some authors have noted the potential for

TABLE III
MECHANORECEPTORS IN THE ANTERIOR CRUCIATE LIGAMENT OF HUMANS

Authors, Method	Types of Receptors	Size of Receptors (μm)	Total No. of Receptors	Location of Receptors, in Ligament	Diameter of Afferent Fibers (μm)
Kennedy et al. ⁸⁵ (1982); non-serial silver-nitrate sections	1 type: free nerve-endings*	Not reported	Not reported	Tibial origin or synovial	Not reported
Schultz et al. ¹³⁸ (1984); serial gold-chloride sections	2 types (Freeman and Wyke ^{41,42}):	200 x 75	1-3	On surface	Not reported
	Type III, Golgi-like Free nerve-endings	Not reported	Not reported	On surface	Not reported
Zimny et al. ¹⁶¹ (1986); 100- μm transverse serial gold-chloride sections	3 types:		"2.5% of total ligament area"	All types: tibial insertion and subsynovial	Not reported
	Ruffini	Not reported			Not reported
	Pacini	Not reported			Not reported
Schutte et al. ¹³⁹ (1987); 100- μm transverse serial gold-chloride sections	4 types:		"1% of total ligament area"	All types: tibial insertion, mid-substance, or subsynovial	Not reported
	2 Ruffini types	Not reported			Not reported
	Pacini (most frequent)	Not reported			Not reported
Halata and Haus ⁶⁶ (1989); electron microscopy	3 types:				
	Ruffini	Not reported	Not reported	Subsynovial	4-6
	Pacini	Not reported	Not reported	Subsynovial	4-8
Haus and Halata ⁷¹ (1990); transverse non-serial glycolmethacrylate sections	3 types:				
	Ruffini	≤ 120	9†	Interfascicular	3-5
	Pacini	≤ 150	12†	Subsynovial	3-5
Amir et al. ³ (1995); 40- μm serial gold-chloride sections	4 types:				
	2 Ruffini types	Not reported	3-6% of periligamentous tissue	All types: only in periligamentous tissue	Not reported
	Pacini	Not reported			Not reported
Sparmann et al. ¹⁴⁶ (1996); monoclonal antibody	Free nerve-endings	Not reported	1-9	Most near femoral insertion	Not reported
	Not reported	Not reported			
	Not reported	Not reported			
Krauspe et al. ⁹⁵ (1995); monoclonal antibody (1 specimen)	2 types:				
	Ruffini	60 x 120	17	Subsynovial and near insertions	Not reported
	Free nerve-endings	Not reported	Not reported	Not reported	Not reported

* A Golgi-like receptor was reported for the posterior cruciate ligament only.

† Number of receptors found in a total of twenty-one anterior-cruciate-ligament specimens.

regrowth of mechanoreceptors, only regeneration of free nerve-endings has been documented^{150,151}. Thick, myelinated fibers have never been shown to form new complex endings such as mechanoreceptors. Existing mechanoreceptors can be reinnervated by means of axonal sprouting but only when circumstances are favorable for guiding the axons, as in a successful nerve suture¹⁰⁵. Even then, only a small proportion of mechanoreceptors (for example, approximately 20 per cent of Golgi tendon organs) are reinnervated. Moreover, these receptors may function abnormally^{10,28}. Current techniques for reconstruction of the anterior cruciate ligament, such as the drilling of bone tunnels into the femoral origin of the ligament, do not create favorable circumstances for axonal sprouting; in fact, the opposite may be the case.

Physiological Studies

In interpreting experimental and clinical work related to the functional loss of mechanoreceptors, two

factors must be considered: the direct effect of loss of receptor output, and alterations in the output of the remaining receptors (mainly those of the capsule). The latter consideration is supported by the findings of Khalsa and Grigg⁸⁶, who studied the responsiveness of capsular mechanoreceptors in cats before and after transection of the anterior cruciate ligament. With use of standardized rotations of the joint, an increase in neural discharge versus joint displacement was seen after transection of the anterior cruciate ligament. This was interpreted as reflecting an increase in capsular stress for a given displacement, which resulted from altered kinematics of the joint.

Unimportant Direct Reflex Effect of Mechanoreceptors on Skeletomotor Neurons

Joint receptors do not have an important direct reflex effect on skeletomotor neurons. Since the 1950s, various authors have attempted to document such an effect of mechanoreceptors of the joint on the muscles surround-

TABLE IV
DISTRIBUTION OF FIBER TYPES IN THE
NERVES OF THE KNEE JOINT IN CATS*

	Medial Articular Nerve	Posterior Articular Nerve
Total no. of fibers	1130	1140
No. of efferent fibers	500	470
No. of afferent fibers	630	670
Percentage of afferent fibers in groups III and IV	91	77

*Modified from the system of Grigg⁵⁷ and excluding group-I fibers.

ing the knee^{4,26,35,141,147}. However, many of these early experiments were confounded by disturbances of muscle or skin receptors. In a well controlled experiment by Grigg et al.⁶¹, a weak positive feedback was demonstrated after terminal extension of the knee (quadriceps facilitation and hamstring inhibition). These findings contradict a putative protective reflex. Furthermore, many injuries occur over a time-frame that is shorter (considerably less than ten milliseconds) than that of monosynaptic reflex responses¹²⁶ (more than twenty milliseconds). Even the weak effect that was noted in the study by Grigg et al. was much less than the effect that was mediated by the afferent-nerve fibers of muscles.

Stimulation of Mechanoreceptors of the Anterior Cruciate Ligament by Hyperextension

Mechanoreceptors of the anterior cruciate ligament are stimulated primarily by hyperextension. Krauspe et al.⁹⁴, in single-fiber studies, identified a total of twenty-six mechanoreceptors of the cruciate ligament among thirteen animals. No activity was seen with the knee in the resting position of 30 degrees of flexion. All fibers responded to movement, primarily extension, with a marked increase in activity if internal or external rotation was added in extension. Activation also was noted during flexion of the knee.

Lack of Convincing Evidence of a Direct Effect of Mechanoreceptors of the Anterior Cruciate Ligament on the Electromyographic Activity of Muscles Surrounding the Knee

Several methods have been used in an attempt to limit mechanical stimulation to the anterior cruciate ligament. Solomonow et al.¹⁴⁴ used traction with a wire loop placed around the anterior cruciate ligament in humans and reported an increase in the electrical activity of the hamstring muscles as measured on electromyograms. Considerable force (130 to 150 newtons) was required as low or moderate force produced no changes. Pope et al.¹²⁵ repeated this experiment in seven cats with loads as high as 125 newtons (four to five times the body weight of the cats). No effect on the electromyographic activity of the quadriceps or hamstrings was

observed, although output in the posterior articular nerve was demonstrated. Normal excitability of reflexes was confirmed with tendon taps, paw pinches, and auditory stimuli. These stimuli easily evoked responses of the quadriceps and hamstring muscles, as seen on electromyograms, in all of the cats. Pope et al. suggested that differences in the method of anesthesia may have induced hyperexcitability in the experiment of Solomonow et al. The use of a loop to pull on the ligament is based on the assumption that no structures other than the intended ligament will be stimulated. Cole et al.²⁷ found this assumption to be questionable. Moreover, increased discharge patterns in the posterior articular nerve occur with as little as thirty micrometers of tibiofemoral motion.

Axial loading with use of traction applied to a block of bone that has been freed along with the tibial insertion of the anterior cruciate ligament seems to be a more appropriate way to isolate mechanical stimulation to the ligament. Miyatsu et al.¹¹² reported electromyographic changes in both the quadriceps and the hamstrings of dogs and cats when traction with forces as high as thirty newtons was applied in this manner. The animals were treated with a precollicular transection (that is, just distal to the thalamus) after removal of the cerebral cortex overlying the mid-portion of the brain and the thalamus. They also had transection of the spinal cord at the mid-thoracic level. It is difficult to interpret these findings as the latency of the changes seems to have been rather long, with the second and largest peak occurring after ten to fifteen seconds. Moreover, the results were not verified with a control experiment after transection of the posterior articular nerve. Therefore, on the basis of the available studies, it must be concluded that an effect of the mechanoreceptors of the anterior cruciate ligament on the electromyographic activity of muscles surrounding the knee has not been convincingly demonstrated.

Influence of Mechanoreceptors of the Anterior Cruciate Ligament on the Output of Muscle Spindles (and Muscle Stiffness) through the Fusimotor System

Johansson et al.⁸¹ investigated the hypothesis of Freeman and Wyke⁸⁰ that ligament receptors influence muscle stiffness through reflex effects involving the fusimotor neurons. Muscle stiffness is defined as the change in length in a muscle-tendon complex for a given change in force. Fusimotor activity was studied indirectly by monitoring the response of 1a muscle-spindle afferent-nerve fibers. These fibers signal the change in the length of the muscle spindles and the speed of this change. An alteration in the response of most of the fibers occurred after traction was applied with use of a wire loop around the anterior cruciate ligament⁸⁰. Control experiments demonstrated disappearance of the reflex effect in the muscle when traction was applied to

TABLE V
CHARACTERISTICS OF TYPES OF FIBERS IN THE NERVES OF THE KNEE JOINT IN CATS*

Type of Fibers	Diameter (μm)	Conduction Velocity (m per sec.)	Medial Articular Nerve	Posterior Articular Nerve	Type of Receptors
Efferent Group IV	0.2-1.5	0.5-2	500	470	Free nerve-endings
Afferent Group I	10-20	80-120	0	27†	Muscle spindle, Golgi tendon organ
Group II	5-15	35-75	57	150	Ruffini, Pacini
Group III	1-5	5-35	132	85	Free nerve-endings
Group IV	0.2-1.5	0.5-2	441	408	Free nerve-endings

*Modified from the systems of Langford and Schmidt⁹⁶ and Martin and Jessel¹⁰⁷.

†These fibers originate in the popliteus muscle.

the posterior cruciate ligament after section of the posterior articular nerve¹⁴³ are caused by direct loss of mechanoreceptors or by altered stimulation of the remaining receptors, or by a combination of the two.

Therefore, there appears to be convincing evidence that afferent-nerve fibers in the ligament influence muscle-spindle afferent-nerve fibers. However, the functional importance of this phenomenon is far from clear.

It may be partly due to the complex input of the fusimotor system⁷⁹. Johansson et al.^{81,82} suggested that the fusimotor system, after integrating input from the afferent nerves of skin, muscles, and joints, serves as a final common path for the regulation of muscle stiffness. Although the fusimotor system has a muscle-reflex effect, it acts only in an indirect manner. After muscle spindles have been activated through the fusimotor system, the skeletomotor neurons (alpha motor neurons) are activated through the 1a afferent-nerve fibers. The indirect route and the low conduction velocity of the fusimotor fibers (fifteen to twenty-five meters per second) probably preclude a protective reflex of the joint, as will be discussed later. It should be emphasized, however, that an indirect route does not imply that the receptors are not important in daily function and athletic performance.

Clinical Studies

Many patients who have an injury of a lower extremity describe vague symptoms such as unsteadiness (giving-way) of the joint. It seems likely that at least some aspects of these symptoms are related to mechanoreceptors. However, this is difficult to document because of the lack of sufficiently sensitive yet measurable parameters. A tear or removal of the anterior cruciate ligament in humans has been associated with neuromuscular changes such as loss of proprioception, alterations in muscle reflexes initiated by the ligament, alterations in muscle stiffness, quadriceps-force deficits, and changes in gait and electromyographic measurements. However, the findings of many studies^{12,75,77,78,88,103} are contradictory, partly because of the different criteria for the selection of subjects and the more or less subtle differences in the parameters or methods of measurement. The question remains as to whether these changes

are caused by direct loss of mechanoreceptors or by altered stimulation of the remaining receptors, or by a combination of the two.

Proprioception in Patients Who Have a Rupture of the Anterior Cruciate Ligament

Proprioception is the sense of position and movement of the limb and is measured in various ways. Two points should be noted with regard to such measurements. First, no current test of proprioception allows differentiation between the mechanoreceptors of the anterior cruciate ligament and the remaining mechanoreceptors of the capsule and muscles surrounding the knee; thus, these tests generally cannot yield conclusive information about the functional importance of mechanoreceptors of the anterior cruciate ligament. Second, mechanoreceptors of the muscles (muscle-spindle receptors) play an important role in proprioception¹⁰⁷. Studies of proprioception after a rupture or reconstruction of the ligament should be interpreted in the broader context of whether mechanoreceptors of the joint or muscles play the primary role in proprioception. Despite extensive reports on this subject during the last two decades, Matthews¹⁰⁸ and Proske et al.¹²⁷ concluded that joint mechanoreceptors (of which ligament mechanoreceptors form only a minority) can signal movement but are unlikely to play a role in position sense. This conclusion is consistent with the absence of mechanoreceptor output in the ligament when the knee is not moving⁹⁴.

Investigators use two types of tests to measure proprioception: those that ascertain the threshold for detection of passive motion (movement sense) and those that examine the capacity to reposition the limb accurately (position sense). Given the complexity of proprioception, neither test is ideal.

In patients who have a torn anterior cruciate ligament, both increased^{12,30} and unaltered^{88,157} thresholds for detection of motion have been reported. Similarly, some authors^{14,30} have found, with use of a repositioning test, differences in the proprioception of patients who have a torn anterior cruciate ligament, whereas others could

TABLE VI
MECHANORECEPTORS IN STRUCTURES OF THE KNEE OTHER THAN THE ANTERIOR CRUCIATE LIGAMENT

Authors, Method	Structure	Description of Receptors*	Eponyms Used
Freeman and Wyke ⁴¹ (1967); cat knee — serial silver and gold-chloride sections	Joint capsule	Freeman and Wyke types I, II, and IV	
Halata and Haus ⁶⁶ (1989); human knee — electron microscopy	Joint capsule	Free nerve-endings Small corpuscle without capsule Corpuscle with connective-tissue capsule Large corpuscle with perineural capsule (resembling Golgi tendon organ) Corpuscle with inner cores and perineural capsule	Ruffini Ruffini Ruffini Pacini
O'Connor and McConnaughey ¹²⁰ (1978); cat knee — non-serial gold-chloride sections	Menisci	Free nerve-endings "2 types of mechanoreceptors"	Not applicable Not reported
Katonis et al. ⁸⁴ (1991); human knee — non-serial gold-chloride sections	Posterior cruciate ligament	Freeman and Wyke types I, II, and IV, mainly near osseous attachments	Ruffini, Vater-Pacini
De Avila et al. ³² (1989); human knee — serial gold-chloride sections	Lateral collateral ligament	Large "spray-shaped" ending; small ovoid endings	"Non-Paciniiform endings"
Andrew ⁵ (1954); cat and rabbit knee — non-serial methylene-blue sections	Medial collateral ligament	Free nerve-endings Variable shape just superficial to ligament and in capsule; thin membrane Thin "plate" shape; closely applied to bundle of connective tissue	Ruffini-type Golgi-type
O'Connor and Gonzales ¹¹⁹ (1979); cat knee — non-serial gold-chloride sections	Medial collateral ligament	Freeman and Wyke types I through IV	Ruffini, Pacini, Golgi

*As reported by the authors. (See Table I for the classification system of Freeman and Wyke⁴¹.)

not find important differences^{44,56}. More recent studies have suggested possible explanations for these reported differences. Several authors found increased sensitivity of proprioception when the knee was in almost full extension^{21,24}. This observation is consistent with the finding that mechanoreceptors of the capsule and the anterior cruciate ligament respond primarily to terminal extension rather than to movement toward flexion in an almost extended knee^{58,61}. A substantial association between proprioceptive deficits after anterior cruciate rupture and meniscal or chondral lesions also has been documented⁴³. These findings confirm that it is not well known which parameters should be investigated in order to demonstrate a diminished sense of the position or motion of the joint, or both, or what exactly is being tested with current types of examinations. Some of the differences in the results of the mentioned studies probably can be explained by differences in the selection of patients, the method of testing, or the specific devices used for testing.

These limitations also apply to studies of proprioception of the ankle and shoulder. Proprioception after sprains of the ankle has been reported as being both decreased^{48,55} and unaltered⁶³. Instability of the shoulder has been associated with a decrease in proprioceptive ability, which was restored with operative treatment^{46,154}.

In both the knee and the ankle, proprioceptive ability sometimes improves with use of an elastic bandage or taping^{79,134,135}. This may partly explain the reports of subjective beneficial effects of bracing of the knee despite the fact that biomechanical studies have indicated questionable effects of bracing on strains of the anterior cruciate ligament in tibial translation or rotation^{18,156}.

Lack of Convincing Evidence of a Ligament-Muscle Reflex in Humans

Abbott et al.³, Gardner⁴⁷, and Palmer¹²³ proposed that motion to the extremes of flexion and extension activates mechanoreceptors of the ligaments, initiating a spinal reflex with contraction of muscles antagonizing the movement (that is, a ligamentomuscular reflex). Such contraction was assumed to take place by direct stimulation of the skeletomotor neurons in order to prevent damage to the ligament and cartilage (a joint protective reflex). In the case of the anterior cruciate ligament, an anterior cruciate ligament-hamstring reflex was proposed⁶⁴. Such experiments do not allow differentiation between afferent-nerve signals emanating from the anterior cruciate ligament, capsule, and muscles. Furthermore, research in animals has not yielded convincing evidence of an anterior cruciate ligament-muscle reflex, and clinical studies with use of anterior

TABLE VII
MECHANORECEPTORS IN OTHER JOINTS

Authors, Method	Structure	Description of Receptors*	Eponyms Used
Freeman and Wyke ⁴² (1967); cat — serial silver and gold-chloride sections	Ankle joint capsule	Freeman and Wyke types I, II, and IV	Ruffini, Pacini
	Ankle ligaments	Freeman and Wyke types I (near osseous attachments), III, and IV	Ruffini, Golgi
Dee ³³ (1969); human and cat — serial silver and gold-chloride sections	Intra-articular fat pad	Freeman and Wyke types I, II, and IV	Ruffini, Pacini
	Hip joint capsule	Freeman and Wyke types I, II (rare), and IV	Not reported
Halata and Munger ⁴⁷ (1980); pigeon — light and electron microscopy	Hip ligaments	Types III and IV	Not reported
	Shoulder joint capsule	Corpuscle consisting of intertwined cylindrical segments	Ruffini
Backenkohler et al. ⁹ (1996); mouse — silver-staining, light and electron microscopy	Shoulder joint capsule	Corpuscle with capsule of several layers and 1 to several inner cores	Herbst
		~30 lamellated corpuscles per joint	Pacini
Vangsness et al. ¹⁵² (1995); human — serial gold- chloride sections	Shoulder ligaments (glenohumeral, coraco- clavicular, coracoacromial)	2 corpuscles of cylindrically shaped branches	Ruffini
		~15 spindle-shaped corpuscles per joint where muscles merge into capsule	Golgi tendon organ
Strasman et al. ¹⁴⁹ (1990); rat — serial silver-stained sections, light and electron microscopy	Elbow joint capsule	Free nerve-endings	Not applicable
		Not reported	Ruffini, Pacini
Stilwell ¹⁴⁸ (1957); human and monkey — serial methylene-blue sections	Wrist joint capsule and ligaments	Free nerve-endings, lamellated corpuscles	Not reported
		“Proprioception triad of Ruffini, Pacini, and free nerve endings”	Ruffini, Pacini
Yahia et al. ^{158,159} ; human — histological sections (1988), scanning electron microscopy and immunohistochemistry (1993)	Interspinous and posterior longitudinal ligaments of lumbar spine	“Relatively deficient in nerves”	Not applicable
		Free nerve-endings	Ruffini
Ahmed et al. ² (1993); rat — immunohistochemistry	Lumbar-facet joint capsule Ligamentum flavum	Globular encapsulated corpuscles	Golgi-like, Ruffini
		Larger corpuscles coiled around blood vessels	Pacini
McLain ¹⁰¹ (1994); human — serial gold-chloride sections	Cervical-facet joint capsule (21 specimens from 3 cadavera)	Encapsulated corpuscles with inner core	Pacini
		Autonomic and sensory fibers	Not applicable
		Autonomic and sensory fibers	Not applicable
		Freeman and Wyke types I (11), II (20), III (5), and IV	Ruffini, Pacini, Golgi

*As reported by the authors. (See Table I for the classification system of Freeman and Wyke⁴¹.)

tibial translation to induce a reflex of the hamstrings extensor torque that was larger than would be expected have yielded conflicting results^{16,77,155}.

Possible Alteration of Muscle Stiffness after a Rupture of the Anterior Cruciate Ligament

In view of the effects of mechanoreceptors on muscle spindles, it is reasonable to presume that such receptors affect muscle stiffness. This concept is based on the model of the muscle-tendon complex as a mass-spring system with a damping component that was described by Hill^{73,103}, although such modeling is not unquestioned⁹⁷. Two studies in which measurements based on this model were used for patients who had a torn anterior cruciate ligament yielded conflicting results^{78,103}.

Loss of Neurosensory Feedback as a Possible Cause of Quadriceps-Force Deficit

Atrophy of the quadriceps is an almost constant finding in patients who have a torn anterior cruciate ligament^{19,83,106,117,160}. Several authors found a decrease in

on the basis of the decrease in the volume of the quadriceps as measured with computed tomography^{37,39,83,99,100}.

The hamstring muscles do not have a comparable force deficit. Specific physiotherapy can only partially correct the deficit¹⁴². The difference in torque has been reported to persist after reconstruction of the anterior cruciate ligament with use of autogenous grafts or allografts from the patellar ligament^{142,159} or with use of semitendinosus grafts^{92,132}.

Under static conditions, the integrated electromyogram reflects the number of activated muscle fibers and their frequency of discharge. Several researchers found a lower summed electrical activity (integrated electromyogram) in the affected limb after both operative treatment (reconstruction with use of a bone-patellar ligament-bone autogenous graft)^{29,39} and non-operative treatment^{26,37,39} in patients who had a torn anterior cruciate ligament. (An integrated electromyogram is obtained from the summed electrical activity of a muscle

in a given period of time. This can be calculated by integrating the surface under the curve of the electromyogram for the time-period.) However, the electrical efficiency of the muscle (the ratio of the integrated electromyogram to work) is unchanged in the affected limb^{29,36,39}. These findings led Elmqvist et al.³⁶ to propose that the deficit in strength is the result of decreased stimulation of the quadriceps muscle in the central nervous system. A decrease in the activation of the quadriceps muscle at a spinal or higher level could be a consequence of an alteration in the afferent signals after a tear of the anterior cruciate ligament.

Gait Analysis

Gait analysis shows functional adaptations in a high proportion of patients who have a tear of the anterior cruciate ligament. Such analysis of patients who have a chronic tear of the anterior cruciate ligament has shown a decrease in the flexion moment of the knee in the range of 0 to 40 degrees of flexion^{7,17}. When the normal limb moves into the mid-stance phase, gravity and inertia generate a moment that tends to flex the knee. This external flexion moment is balanced by the quadriceps muscles (internal extension moment); therefore, a decrease in the flexion moment suggests a decrease in the quadriceps muscle moment⁶. Such a decrease was seen in both limbs of patients who had only one knee with a torn anterior cruciate ligament¹⁷. Andriacchi⁶ termed this finding the quadriceps-avoidance gait. Not all patients who have a torn anterior cruciate ligament have such a gait. Its prevalence is partly related to the time since the injury¹⁹. In activities that involve knee-flexion angles of less than 30 degrees (that is, those involving normal gait), the quadriceps-avoidance gait is most effective in preventing anterior tibial translation^{6,110,111}. In activities that involve knee-flexion angles of 40 degrees or more (for example, jumping or sharp changes in running direction), increased contraction of the hamstrings is effective in preventing anterior tibial translation^{111,113,122,129}. Both mechanisms precede the event that they are meant to antagonize. This is possible only if the joint-capsule receptors that signal the event transfer information to higher centers, followed by modification of motor programs (that is, a learning process). Conversely, reflex-like mechanisms can be excluded on the basis of the time-frames that are involved¹²⁶. It is assumed, although not yet proved, that these functional adaptations are beneficial to patients who have a torn anterior cruciate ligament.

Functional Adaptations after a Tear of the Anterior Cruciate Ligament to Prevent Damage to Secondary Restraints and to Stabilize the Knee during Stressful Activities

The prevalence of secondary meniscal lesions and associated degenerative joint disease in patients who have a torn anterior cruciate ligament¹¹⁵ seems to confirm

the increased stress on the menisci in a knee with a torn anterior cruciate ligament¹¹¹. A decreased quadriceps moment in patients who have a quadriceps-avoidance gait thus may be a protective mechanism for the secondary restraints. The development of a quadriceps-avoidance gait may depend on chronic stretching of the joint capsule, but it probably also depends on other factors, such as the ability of motor programs (neural networks that govern specific, often repeated motions) to adapt to a changing stimulus. Additional support for this concept is found in studies of dogs in which the anterior cruciate ligament was transected. Kinematic studies demonstrated increased anterior tibial translation throughout the stance phase after transection of the anterior cruciate ligament in dogs. The dogs compensated by decreasing the limb load and increasing flexion of the knee throughout the gait cycle, but they were unable to prevent subluxation of the joint in the stance phase⁹⁰. (Because the dogs were studied six weeks after transection of the anterior cruciate ligament, it is not known whether functional adaptations would have developed.) Transection of the anterior cruciate ligament leads to slight degenerative changes in the cartilage, but additional deafferentation of the knee joint produces severe degenerative changes^{121,153}. This suggests that sensory input from the joint may play a role in adapting movement strategies so that potentially harmful positions and loads are prevented, thus decreasing the rate at which an unstable joint degenerates.

Overview

It can be presumed that injuries to ligaments have two neurosensory effects: a loss of signaling from the mechanoreceptors in the torn ligament and a gain in signaling from the mechanoreceptors in the periarticular tissues as a result of instability. The fact that the functional outcome of a torn anterior cruciate ligament is not directly associated with the amount of laxity may be related to the variable adaptation of patients to loss or gain of signals. We propose the following.

1. Mechanoreceptors in ligaments are part of a complex of several receptor populations providing input that influences muscle stiffness. The fact that several other (potentially redundant) receptor populations have input into this system can be used to argue that the relatively few receptors in most ligaments are of minor importance in this context and that the loss of receptor input may be compensated for by the remaining receptors. However, the precise role of various receptors may vary from individual to individual, so loss of mechanoreceptors or failure to adapt by means of redundant sources may be more critical in some patients than in others.

2. Specific considerations for the quadriceps may be justified. The anterior cruciate ligament and the quadriceps are mechanical antagonists. Extension of the knee generates strain in the anterior cruciate ligament.

activating mechanoreceptors in the ligament. Contraction of the quadriceps muscle further increases anterior-cruciate-ligament strain in the extended knee. The anterior cruciate ligament is the only structure that specifically antagonizes the anterior tibial translation generated by the quadriceps muscle; thus, its mechanoreceptors may be the only ones that sensitively and effectively signal anterior tibial translation. It therefore seems reasonable to assume that the output of the anterior-cruciate-ligament mechanoreceptors has a specific influence on the function of the quadriceps. The fact that only a few mechanoreceptors are present need not signify that the receptors are unimportant as they may be the only receptors that are involved in this function. On the basis of the quadriceps-force deficit after a tear of the anterior cruciate ligament, it can be hypothesized that this proposed function may facilitate activation of the quadriceps when the anterior-cruciate-ligament strain is within certain limits. Assuming that a direct reflex influence is unlikely, it might be proposed that the output of the anterior-cruciate-ligament mechanoreceptors has a modulating effect on motor programs in which the quadriceps muscle plays an important role. Traditional views have been based on the concept of direct reflexes, but it may be more realistic to incorporate the concept of a history of loading instead of a single loading event into any hypothesis

regarding the function of such receptors.

3. On the basis of the neuropeptide expression of afferent free nerve-endings, it appears that these fibers may play a role, in conjunction with the efferent fibers, in maintaining homeostasis of the ligament (or a remodeled graft): that is, they may play a role not only in the regulation of blood flow but also in the turnover of collagenous tissues. Whether a mechanoreceptor-mediated response to the loading history of the ligament also contributes to this is entirely speculative.

Potentially testable hypotheses could be formulated for all three proposed functions. Most of the necessary experiments will have to be based on selective blockade of the afferent-nerve fibers of the anterior cruciate ligament in combination with a sensitive outcome measure. It seems likely that the mechanoreceptors of ligaments associated with other joints will be comparable with those of the anterior cruciate ligament, with regard to the first and third functions. What seems obvious is the presence of mechanoreceptors and their clear roles in functions that are subtle or difficult to measure. However, such subtlety cannot be taken to mean that mechanoreceptors do not have important implications for function or performance. As more sensitive measures are developed, it will be possible to study the true roles of these receptors and to determine what must be done to facilitate recovery after their loss.

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