

Characteristics of Hip Joint Mechanoreceptors in the Cat

ALESSANDRO ROSSI AND PETER GRIGG

Department of Physiology, University of Massachusetts, Worcester, Massachusetts 01605

SUMMARY AND CONCLUSIONS

1. Capsule afferents in the hip discharged only when the joint was rotated into its limit of movement along a single axis of rotation.

2. The optimal axis of rotation for an afferent was determined by the part of the capsule that was loaded by the rotation and by the location of the receptor in the capsule. Afferents were activated by rotations along the axes of abduction, adduction, and internal and external rotation.

3. Less than 3% of the afferents sampled responded to flexion or extension of the hip, even using extreme rotations.

4. Neurons located in the posterior and anterior regions of the capsule were studied quantitatively using as stimuli axial rotations of the femur, which load those regions of the capsule. Responses of afferents are described in relation to joint angles and torques. Thresholds for activation and saturation of slowly adapting responses of neurons are described.

5. Evidence is presented that "full-range" joint afferents, described by others in the hip joint, are afferents from the gemellus inferior muscle.

6. It is concluded that capsule afferents serve as "limit detectors," which signal proximity of the joint to its limit of rotation.

INTRODUCTION

Mechanically sensitive neurons innervating joint capsules have been studied for many years, and some conflicts have developed as to the stimuli to which they are sensitive (2, 4, 8, 25). In recent years there have been a number of reports (4, 16, 22, 27) that

indicate that capsule afferents are sensitive primarily to rotations of a joint into a limit of its range of movement. For such movements it is possible to construct a simple model for the activation of capsule afferents. In a freely moving joint, rotations through intermediate or midrange joint angles are not constrained by the joint capsule. Thus the joint rotates freely and while the capsule is deformed, it is not subjected to any extrinsic loading. When rotated beyond the midrange into a limit, the capsule becomes loaded and restricts further rotations. With the capsule loaded, the joint is at its limit of rotation. Afferents in the capsule respond when the capsule is stretched by the applied load, and thus they function as capsule load detectors or as limit detectors.

Supporting this model are observations that in the knee, the posterior capsule is loaded at the limit of extension movements and limits extension rotation of the joint (3, 11, 16, 28). Furthermore, capsule afferents in isolated knee posterior capsule have been shown to respond to proportion to applied loads and not to respond when the capsule is not loaded (18). The above model is also consistent with findings of capsule afferents from ankle and wrist joints (22, 27), where most afferents have been shown in discharge at the limit of rotations. However, a recent report of the properties of hip joint afferents (5) cannot be reconciled with the above model. Carli et al. (5) described full-range afferents from the hip capsule, afferents that discharged at all angles of the joint and whose discharge was modulated with rotations in all axes. From these observations, Carli et al. (5) concluded that hip joint afferents, unlike afferents from other joints, were able to encode the position of the hip

joint. Furthermore, in a subsequent paper (7) they concluded that capsule afferents were better able to encode joint angle than were muscle (gluteus medius) afferents. These findings (5, 7) are not consistent with observations that position sense in the human hip is altered minimally, if at all, by total capsulectomy (17). Further, such full-range capsule afferents could be consistent with the capsule loading model only if *a*) receptors in hip capsule were qualitatively different from those in other joints, or *b*) if the hip capsule were mechanically different from the capsules of other joints.

In an attempt to determine the basis for the apparent difference in properties of mechanoreceptors in the hip and other joints, Carli et al. (6) recently recorded from hip posterior articular nerve (PAN) afferents in a preparation in which the hip capsule was exposed, cut free from its bone attachment at one end, and a strip of innervated capsule was subjected to loads in an experiment similar to those reported recently in knee capsule (18). Hip capsule receptors were not found to be qualitatively different from knee capsule receptors studied under similar conditions: afferent responses were a function of applied load. A significant observation in those experiments was that the hip PAN contains large numbers of afferents from the gemellus inferior (GI) muscle, which covers the posterior surface of the hip capsule. Those muscle afferents were present in the PAN in the earlier study of Carli et al. (5), raising the possibility that the full-range afferents in that study were afferents from the GI muscle.

In this report we describe a new investigation of the properties of capsule receptors from the hip. This study differs from Carli's (5) earlier study of hip afferents with respect to methods, as we have used a preparation of the hip PAN in which muscle afferents have been scrupulously eliminated from the hip PAN by excision of the GI muscle. Furthermore, we have isolated the medial articular nerve (MAN) of the hip joint, which innervates the inferior and anterior regions of the capsule, and we report here the properties of afferents from both PAN and MAN.

METHODS

Preparation

ANESTHESIA AND MAINTENANCE OF ANIMALS. Cats were anesthetized with an intraperitoneal dose of Nembutal (35 mg/kg). Anesthesia was maintained with intravenous doses of Nembutal as required. Rectal temperature was maintained at 37.5°C using a thermostatically controlled hot-water heating pad and a heat lamp.

ISOLATION OF PAN AND POSTERIOR CAPSULE. The initial preparation of the PAN was done generally following the method of Carli et al. (5). However, since the preparation of the PAN is of central importance to this paper, it is described in full detail. A skin incision was made over the region of the head of the femur. The sciatic nerve was then exposed in the region of the hip by cutting the femoral insertions of, and reflecting, the caudofemoralis, gluteus maximus, gluteus medius, tensor fascia latae, and piriformis muscles. The sciatic nerve was sectioned just above the exit of the hamstring nerve. The nerve to the quadratus femoris muscle was isolated and cut between the bellies of the internal obturator and the quadratus femoris (QF) muscles. The central component of the QF nerve runs through the GI muscle. As it runs in the GI, it gives off a series of small branches. Some of the branches innervate the posterior aspect of the hip joint capsule (12) and others innervate the GI muscle (6). The branches that innervate the capsule are collectively called the PAN (12).

Where the QF nerve joins the sciatic, it was dissected free from the sciatic nerve for a distance of about 15 mm in order to provide space for stimulating electrodes. Next, the obturator internal muscle was removed so as to expose the underlying gemellus inferior muscle. The GI muscle covers the posterior region of the capsule. It was excised as follows: First, the tendon was cut at its femoral insertion and reflected back. Some of the fibers of the GI muscle insert directly into the ischiatic surface of the joint capsule (10); these fibers were then excised. Groups of muscle fibers were cut from the capsule surface and dissected back toward the ischium. A small amount of the GI muscle was left intact along the ischium in order not to injure the QF nerve. The end result of this procedure was that the QF nerve innervated only the posterior capsule, and the posterior surface of the capsule was exposed. The exposed capsule surface was maintained under moist gauze and exposed only when necessary for stimulation of the capsule surface.

ISOLATION OF MAN AND INFERIOR CAPSULE. The MAN branches from the obturator



FIG. 1. Schematic representation of the hip capsule and its innervation, showing their relationship to the pelvic bones. Shaded area, hip capsule. a, PAN arises as anterior branches from the quadratus femoris nerve. Posterior branches arising from the same nerve innervate the gemellus inferior muscle. b, MAN arises as a small anterior branch from the terminal branches of the obturator nerve, just beyond its emergence from the obturator foramen.

nerve as it passes through the obturator foramen (12). In order to isolate this branch we first exposed the obturator nerve as follows: The femoral tendon of the obturator external muscle was cut where it lies between the femoral insertions of the obturator internal and quadratus femoris muscles, and the muscle was reflected back. This made it possible to visualize the inferior section of the capsule and also made it possible to see the obturator nerve passing through the obturator foramen (see Fig. 1). After passing through the obturator foramen, the obturator nerve divides into branches that innervate the obturator external, adductor femoris, adductor longus, pectineus, and gracilis muscles. All of these branches were cut. According to Dee (12), the MAN emerges from the lateral branch of the obturator nerve before that branch ramifies into the pectineus and adductor femoris nerves. Thus by cutting the individual muscular branches of the obturator nerve, we were able to leave just the MAN intact.

The anterior surface of the capsule was exposed in some experiments by cutting the belly of the capsularis muscle as it crosses the joint capsule. Rectus femoris and vastus lateralis muscles were deflected anteriorly to allow space for viewing and probing the anterior surface.

The superior surface of the capsule was exposed

in some experiments. The femoral insertion of the gemellus superior and gluteus maximus muscles were cut and both muscles reflected in order to expose the superior surface of the capsule. The innervation of the superior capsule was variable and often innervated from superior branches of the PAN.

We did not routinely expose all of the surfaces of the capsule, preferring instead to restrict the area of capsule studied, leaving most of the muscles intact in order to maintain the position of the femur and ischium in as normal a relationship as possible.

FURTHER DENERVATION OF LIMB. In order to reduce neuronal activity in the L₇ and S₁ dorsal roots, the hindlimb was denervated as thoroughly as possible. In addition to the denervation of muscles as listed above, the following nerves were also cut: on the lateral side of the limb, all of the branches of the sciatic nerve (superior gluteal nerve, inferior gluteal nerve, and the nerve to obturator internal and gemellus superior) were cut except for the branch of QF. On the medial side of the leg, the femoral and the lateral femoral cutaneous nerves were cut. Also, we cut the dorsal rami of spinal nerves, which innervate the lumbar portions of the longissimus dorsi muscle.

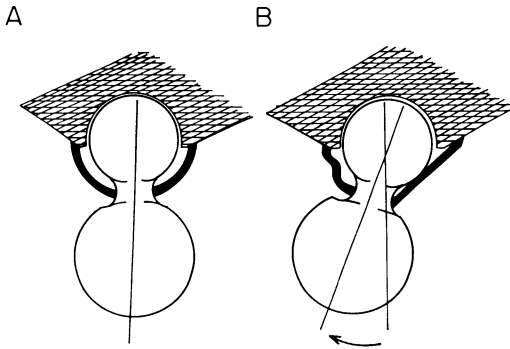


FIG. 2. Schematic representation of the left hip joint, as viewed from above, to illustrate deformations of the capsule produced with axial rotation of the femur. Hatched area represents the ischium. Heavy lines represent the capsule, coupling the rim of the acetabulum to the neck of the femur. A: joint in neutral position. B: internal rotation of the femur. The posterior capsule is loaded and the anterior capsule is unloaded.

A lumbosacral laminectomy was performed to expose the L_7 and S_1 dorsal roots. The skin was used to form a pool, which was filled with warm mineral oil. The L_7 and S_1 dorsal roots were cut at their entry to the spinal cord and reflected. The roots were then divided into small bundles for subsequent recording. Small filaments were placed on platinum wire electrodes for recording. The methods used for recording neuronal discharge are described elsewhere (18).

Stimulation of afferents

IDENTIFICATION OF AFFERENTS. When a dorsal root filament was recorded from, the capsule was stimulated in order to determine whether capsule afferents were present. The limb was rotated in order to see if any silent neurons could be brought to discharge or if any spontaneously active discharge could be modulated. The rotations used for searching were as follows (see Figs. 2, 3, and 4 for reference):

Axial rotations. These are rotation about the long axis of the femur. Internal rotation (IR) (see Figs. 2 and 4) is clockwise rotation of the left femur when looking down on the animal; external rotation (ER) is a counterclockwise rotation.

Abduction and adduction. Abduction is rotation of the hip such that the femur is moved laterally away from the body (see Figs. 3 and 4). Adduction is rotation such that the femur is moved toward the body.

Flexion and extension. These are movement of the femur in a plane parallel to the body of the cat.

When testing for the presence of afferents in filaments, we rotated the limb to its limit in each

axis. These rotations were firm but not forceful manual movements. Similar axial rotations were accomplished with the rotator stimulator with torques in the range of 1,000–1,500 g-cm.

In addition to rotation of the femur, we also probed the capsule surface using a blunt glass rod. No neurons were included in the sample unless they could be driven by discrete, localized probing of the capsule surface. This is an important criterion because it was never possible to denervate the leg completely, and in every experiment afferents from muscles around the hip were observed in great numbers. We occasionally observed afferents that were driven either irregularly or very weakly when the capsule was probed. We investigated such neurons very carefully and in every case localized the receptor in muscles coupled across the hip. We presume that these neurons were activated by coupling of muscles to the capsule. Most of these afferents were spontaneously active, and all were activated by intravenous injections of succinylcholine (SCH), 0.05 mg/kg.

STIMULATION OF AFFERENTS—ROTATION OF HIP. *Characterization of general properties of afferents.* When a capsule afferent was isolated, its general properties were studied in relation to limb positioning, using manual movements of the femur.

Quantitative studies of responses to rotations. Quantitative studies of stimulus-response relationships were undertaken on those neurons that were sensitive to external or internal (axial) rotations. The femur was fixed in a stimulator (shown in Fig. 4) that produced known axial rotations while allowing for measurements of both joint angle and the resulting torque. Angular displacements were produced with a small stepping motor. Angular velocity was always $10^\circ/\text{s}$. Dis-

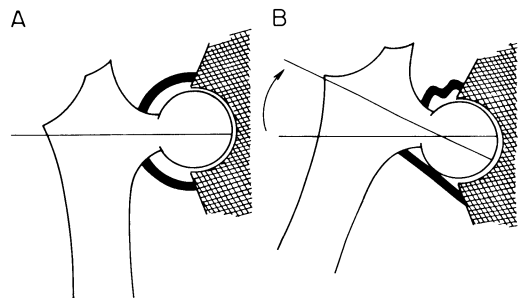


FIG. 3. Schematic representation of the hip joint, as viewed from behind the joint, to illustrate deformations of the capsule produced with abduction. The format is the same as in Fig. 2. A: joint in neutral position. B: abduction of the femur. The inferior capsule is loaded and the superior capsule is unloaded.

placements were measured with a potentiometer and torque was measured by strain gauges on flexible elements that coupled the driver to the shaft to which the femur was clamped. This device was

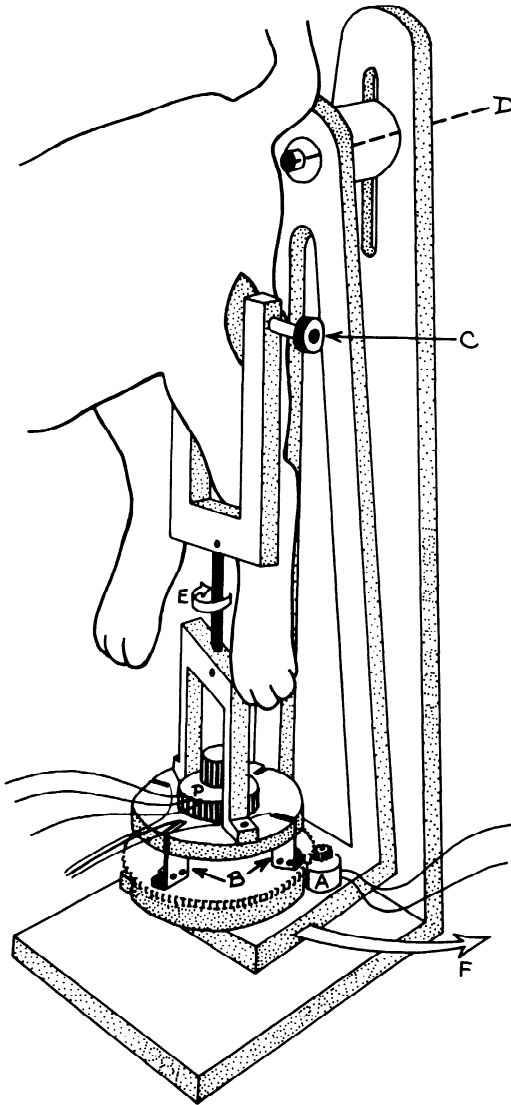


FIG. 4. Apparatus used to rotate the hip joint in external and internal rotation. Rotation of the shaft E produces axial displacements. Direction of arrow E indicates internal rotation. The femur can also be statically held in ab- or adduction by rotation about the axis D. Arrow F indicates abduction of the hip. A, stepping motor; B, flexible elements that couple the driver to the actuating shaft E; strain gages on these elements measure torque. C, clamp that couples stimulator to the femur; P, potentiometer to measure angular displacements.

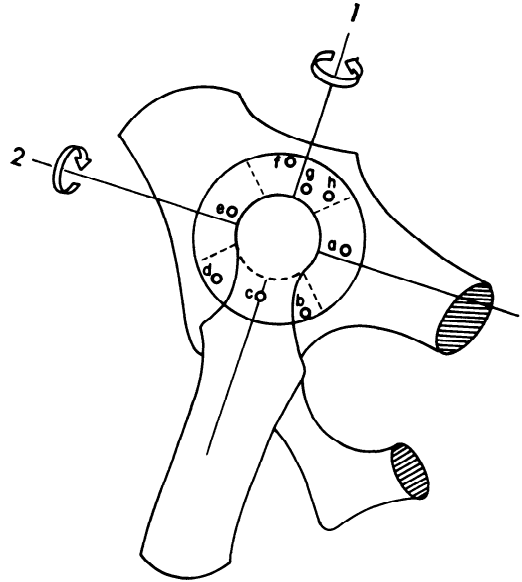


FIG. 5. Properties of receptors associated with location in capsule. The circle represents the capsule as if cut from the acetabular attachment and reflected outward as a sheet. 1, long axis of the femur. Rotation about this axis constitutes external rotation (direction of arrow) or internal rotation (opposite arrow). 2, orthogonal axis. Rotation about this axis in the direction of the arrow is abduction. Opposite direction is adduction. Dashed lines divide each quadrant of the capsule into halves. a-h: locations of eight receptors in the capsule. Below are listed the optimal rotation to excite each receptor (receptor, identification, location in capsule, and optimal stimulus): a, 8-3-N2, posterior, IR only; b, 8-17-N6, posterior-inferior, IR plus ABD; c, T1206, inferior, ABD only; d, 8-10-N10, inferior-anterior, ER plus ABD; e, 8-13-N7, anterior, ER only; f, 8-11-N9, superior-anterior, AD plus ER; g, 8-11-N2, superior, ADD only; h, 8-11-N7, superior-posterior, ADD plus IR.

operated under computer control using an LSI-11 computer: operation of the motor and acquisition of angle, torque, and neuronal output signals were all accomplished under program control. In multineuronal recordings, the discharges of individual afferents were discriminated on the basis of action potential shape (23). In order to minimize interactive effects between successive stimuli, 4-min intertrial intervals were used.

Precisely determined displacements could be produced only in axial rotation with this device. The leg could also be statically positioned in adduction-abduction or in flexion-extension, in order to optimize the response of afferents that did not respond maximally to pure axial rotations.

There were some afferents that could only be activated with combinations of abduction and internal rotation. Often the appropriate stimulus for

such afferents could not be produced using the roatator stimulator. In these neurons, thresholds for activation were measured by manually holding the limb in abduction and producing axial rotation with a hand-held torque meter (Power Instruments), which was coupled to the femur.

MEASUREMENTS OF CONDUCTION VELOCITY. Conduction velocity of afferents from the posterior region of the capsule, whose afferents run in the PAN, were measured conventionally by electrically stimulating the PAN. The MAN, however, was not accessible for such electrical stimulation. Because of its location and its short length, attempts at electrical stimulation usually resulted in activation of the whole obturator nerve. Usually this resulted in a dorsal root compound action potential so large that responses of individual afferents could not be discriminated. Therefore, in these cases conduction velocity was measured by directly stimulating the capsule surface at the receptive field of the afferent.

RECORDINGS FROM GEMELLUS INFERIOR AFFERENTS. In an attempt to reconcile our observations with those of Carli et al. (5), we replicated their experimental protocol in three experiments and recorded from identified afferents from the GI muscle. In these experiments, the preparation was identical to that of the PAN (above) except that the GI muscle and the obturator external muscle were left intact.

RESULTS

Ninety-two capsule afferents were recorded in 17 successful experiments. Afferents were categorized as quickly adapting or slowly adapting on the basis of their response to a static stimulus.

Quickly adapting afferents

Twenty-two of the afferents were quickly adapting (QA), having discharge that adapted to zero in 4 s or less. Of these, four were Pacinian corpuscle- (PC) like, responding to capsule probing or to rotations with a short, high-frequency burst of 4–7 impulses. PC-like afferents could also be activated by tapping the table or the apparatus. PC-like afferents had no specificity for rotations along different axes: they responded equally to movement of the femur along any axis. The other QAs, however, were similar to slowly adapting afferents (below) in that they responded to rotations of the leg along only a single optimal axis. The nature of this sensitivity to rotations was similar to that observed in slowly adapting afferents, as described below.

Slowing adapting afferents

GENERAL PROPERTIES. The remaining 70 afferents were slowly adapting, responding to an appropriate static stimulus with a maintained discharge. In all cases the appropriate stimulus to activate neurons was rotation into a limit of movement. No afferent discharge was observed when the femur was in a neutral position (e.g., the position achieved when the denervated leg is allowed to hang passively). Further, all of these afferents responded only when the hip was rotated along a single optimal axis. Afferents were found to be sensitive to internal or external rotation and abduction or adduction. Only two neurons responded to pure flexion or extension rotations and are discussed later.

DETERMINANTS OF SPECIFICITY OF AFFERENTS TO ROTATIONS ALONG DIFFERENT AXES. A given afferent discharged only when the joint was rotated along a specific axis. The type of rotation that activated a given afferent was determined by the location of the receptor in the capsule and by the geometry of the joint and the joint capsule. The hip joint is a ball-and-socket joint, and the femoral ball is offset from the femoral shaft, being connected to it by the neck of the femur (see Fig. 3). The capsule extends from the rim of the acetabulum to the neck of the femur. The ways in which the capsule is deformed when the femur is rotated are shown schematically in Figs. 2 and 3. As can be seen (Fig. 2), axial rotations reciprocally load and unload the anterior and posterior regions of the capsule. Likewise (Fig. 3), abduction and adduction reciprocally load and unload the superior and inferior regions. Afferents from capsule receptors are activated by those rotations that stretch the region of capsule in which they reside. For example, internal rotation (Fig. 2) stretches the posterior capsule and activates only those receptors that reside in the posterior capsule. Similarly, receptors in the inferior capsule are excited only by abductions (Fig. 3), while those in the superior capsule are activated only by adductions. Figure 5 shows a summary of the properties of eight afferents whose receptors were located in different capsule regions. In this figure, receptive fields are shown on a circle, which represents the hip capsule. The cap-

sule is represented as if it were cut from the acetabular attachment and reflected toward the neck of the femur. As may be seen, each afferent was sensitive only to those rotations that, as described above, would load the region of capsule where the receptor is located. Receptors located in the posterior capsule (e.g., a) were activated by internal rotation, receptors in the inferior capsule (e.g., c) by abduction, receptors in the anterior capsule (e.g., e) by external rotation, while receptors in the superior capsule (e.g., g) were activated by adduction of the femur. However, only those receptors whose locations coincided with the vertical axis or the horizontal axis of the capsule (e.g., a, c, e, f) were activated by a simple rotation such as pure IR or pure abduction. Capsule regions intermediate between the above axes would be optimally stretched by a rotation that involved both axial and abduction-adductive rotation. For example, neuron b in Fig. 5 would be activated when the neck of the femur is displaced upward and to the left, which is accomplished by internally rotating and abducting the femur. The other receptors indicated in Fig. 5 (d, f, h) were, similarly, activated only by combinations of axial rotations and adduction or abduction. It is an important observation that there were no exceptions to this scheme. We observed two afferents that were activated by flexion or extension movements. Responsiveness to flexion and extension movements was tested using rotations to the limits of these movements. We were unable to rotate the femur beyond 45° (flexion) and 145° (extension) because the resulting movements of the spinal cord upset our recording situation. In the two neurons that responded to flexion or extension, the response was always less than that of the same afferent to an axial or abductive rotation.

STUDIES OF RELATIONSHIP BETWEEN STIMULUS AND RESPONSE. We undertook detailed studies of the relationship between stimulus and response in 41 neurons. These studies by design were limited to neurons located in the posterior capsule and activated by internal rotation. When an afferent was isolated and its general properties cataloged, the limb was fixed in the axial rotator. The femur was then rotated to preset angles and neuronal discharge and loads were recorded.

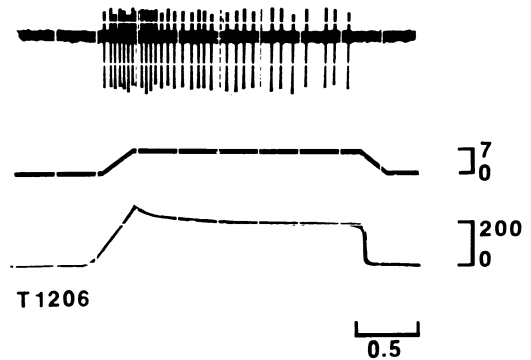


FIG. 6. Response of a single capsule afferent to internal rotation of the femur. Receptor was located in the posterior capsule. Top trace, action potentials from afferent. Middle trace, angular displacement (deg). Bottom trace, torque (g-cm). Time marker, 0.5 s.

Figure 6 shows the response observed in one neuron when the femur was internally rotated. The relationship between neuronal discharge and joint angle and applied load (torque) for this neuron is shown in Fig. 7. This neuron had a threshold for activation at an angle of 10°, which corresponded to an applied torque of 400 g-cm. As may be seen, the response increased with increasing stimulus magnitude and saturated above 950 g-cm. In the 41 afferents that were studied using axial rotation, all had these general features. Thresholds for activation varied between afferents; a histogram of threshold angles is shown in Fig. 8. The modal value for threshold was 10°. Only 10 afferents had thresholds less than 10°. Thresholds for saturation were observed in 30 afferents, and a histogram of saturation thresholds is shown in Fig. 9.

Sensitivity of afferents to rotations was measured as the slope of the curves drawn in Fig. 7 (using values from the threshold up to the peak). Sensitivities ranged from 0.5 to 6.6 impulses \cdot s $^{-1}$ \cdot deg $^{-1}$, mean = 1.9. Expressed in terms of torques, sensitivities ranged from 0.01 to 0.5, impulses \cdot s $^{-1}$ \cdot g-cm $^{-1}$, mean = 0.04.

AFFERENTS RESPONDING TO ROTATIONS IN AXES OTHER THAN INTERNAL ROTATION. Afferents located in the anterior capsule and sensitive to external rotation were also studied using the limb rotator stimulator. With regard to thresholds and sensitivities, these afferents were not different from afferents

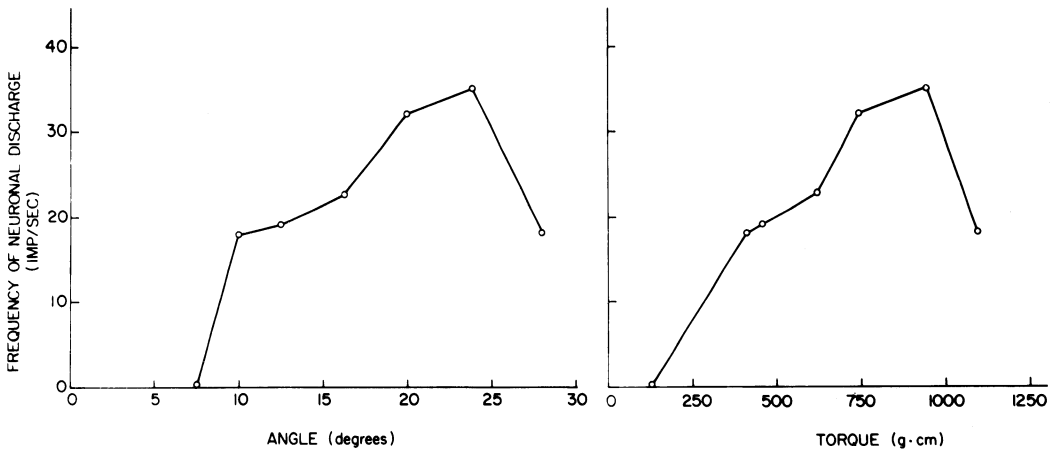


FIG. 7. Frequency of neuronal discharge plotted versus joint angle (internal rotation) on left and versus torque on right. Same neuron as in Fig. 6.

from the posterior capsule responding to internal rotations. An example of the response of one such neuron is shown in Fig. 13. Because the stimulator was designed to rotate the femur only in axial rotation, afferents from other capsule locations were studied only qualitatively. As an example, one neuron located in the inferior capsule (c in Fig. 5) was studied by rotating the limb in abduction while measuring joint angle using a protractor. Results from this neuron are shown in Fig. 10 and were not qualitatively

different from the other afferents that we describe. Twenty-two other afferents located in the superior and inferior regions of the capsule were studied only qualitatively but did not differ perceptibly from the anterior and posterior capsule afferents described above.

RESPONSES OF CAPSULE AFFERENTS TO SUC-CINYLCHOLINE. In 104 afferents (78 capsule, 26 muscle), we tested the effect of intravenous injections of small doses (0.05

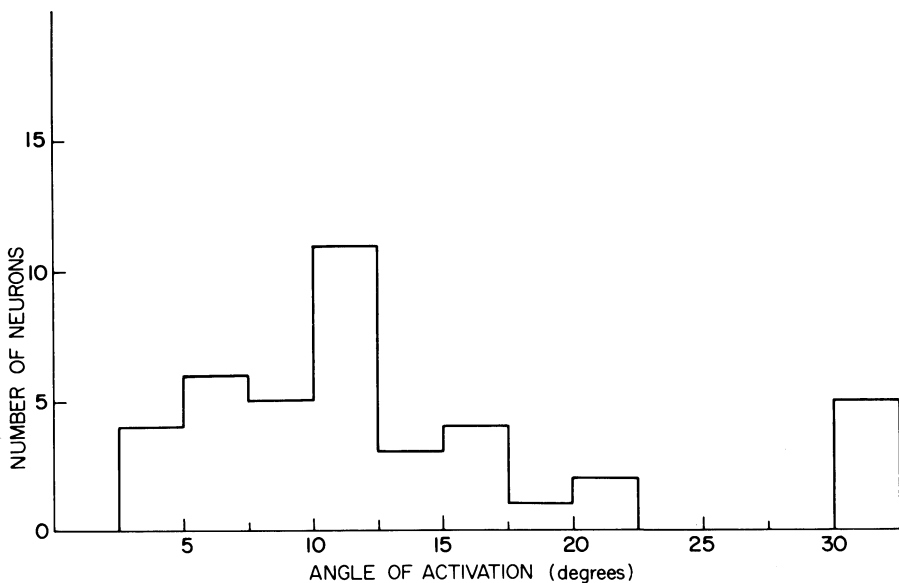


FIG. 8. Histogram of activation angles (internal rotation) for 41 afferents studied with hip rotator.

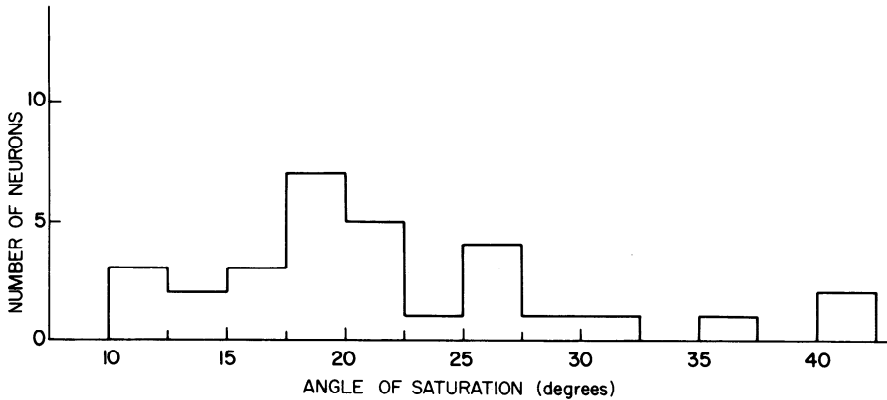


FIG. 9. Histogram of angles at which saturation of response was observed in 30 of afferents from Fig. 8.

mg/kg) of SCH. Similar to results observed by others (4, 16, 22, 27) in other joint capsules, no responses to SCH were observed in capsule afferents. Muscle afferents recorded simultaneously responded vigorously to the same doses (13, 26). Figure 11 shows the response of simultaneously recorded muscle and capsule afferents following SCH administration.

LONG-TERM SURVIVAL OF AFFERENTS. We wished to demonstrate that the properties of afferents observed in these experiments did not represent the properties of deteriorating receptors injured in the process of isolating

the capsule surface. In several experiments continuous recordings of a single neuron were made for long periods of time in order to look for loss of responsiveness that might reflect injury. Stable responses were observed, as shown in data from one afferent in Fig. 12. Many afferents were studied for periods up to several hours in duration without any change in their properties.

We were also concerned that the properties of receptors in the capsule might be affected by the extensive surgery that was used in some experiments to expose the obturator nerve, MAN, and the anterior, inferior, and

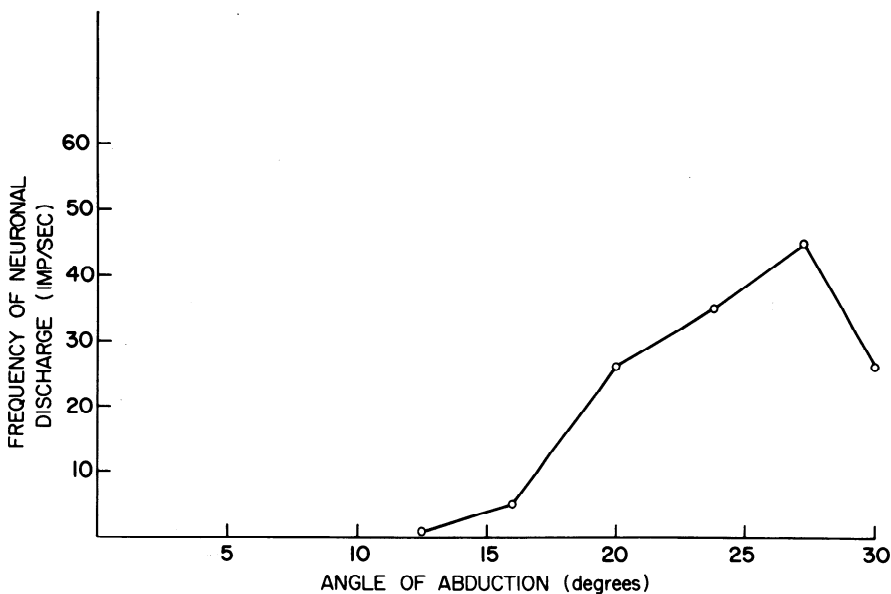


FIG. 10. Response of an afferent located in the inferior capsule to abduction of the femur.

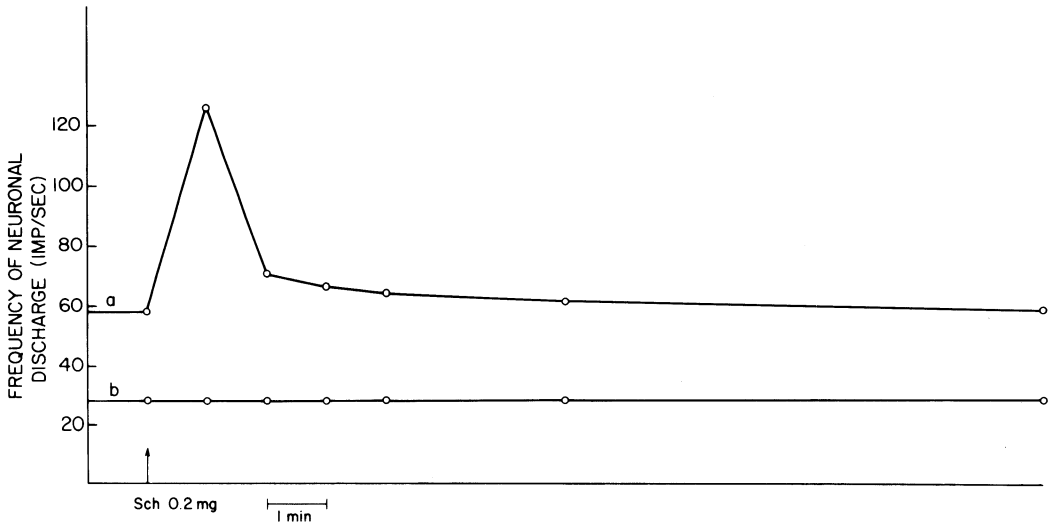


FIG. 11. Responses of GI muscle (a) and posterior capsule (b) afferents to intravenous administration of SCH. The dose of SCH was 0.05 mg/kg. Each point represents the response to an identical internal rotation of the femur.

superior regions of the capsule. However, it was found that in preparations with extensive surgery, the properties of afferents were not different from those in experiments using more conservative surgery. In the four experiments in which the entire surface of the capsule was exposed, 37 afferents were re-

corded. Seventy-eight percent were slowly adapting, as compared to 76% in the whole population. Thresholds of activation were not strictly comparable to thresholds in other experiments, since most of the afferents in these experiments were in the superior, inferior, and anterior capsule. However, the

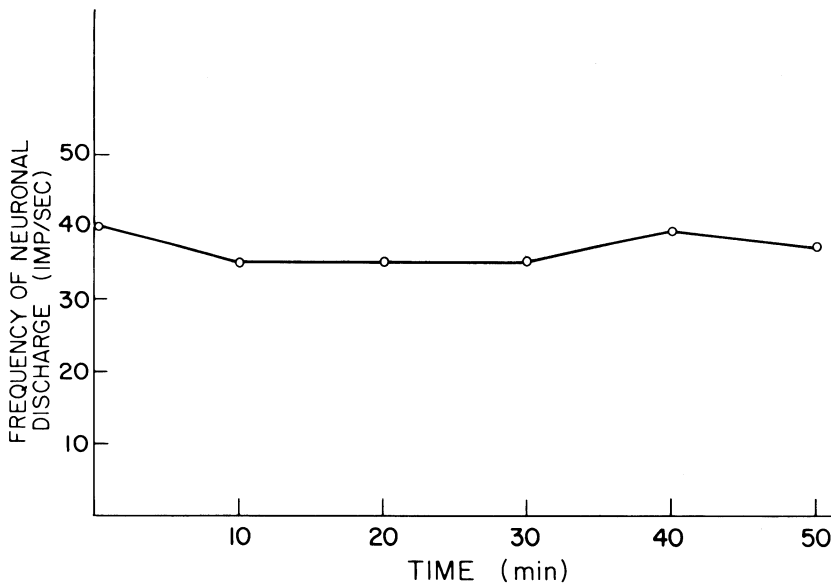


FIG. 12. Response of a single posterior capsule afferent to repeated presentations of an identical internal rotation stimulus.

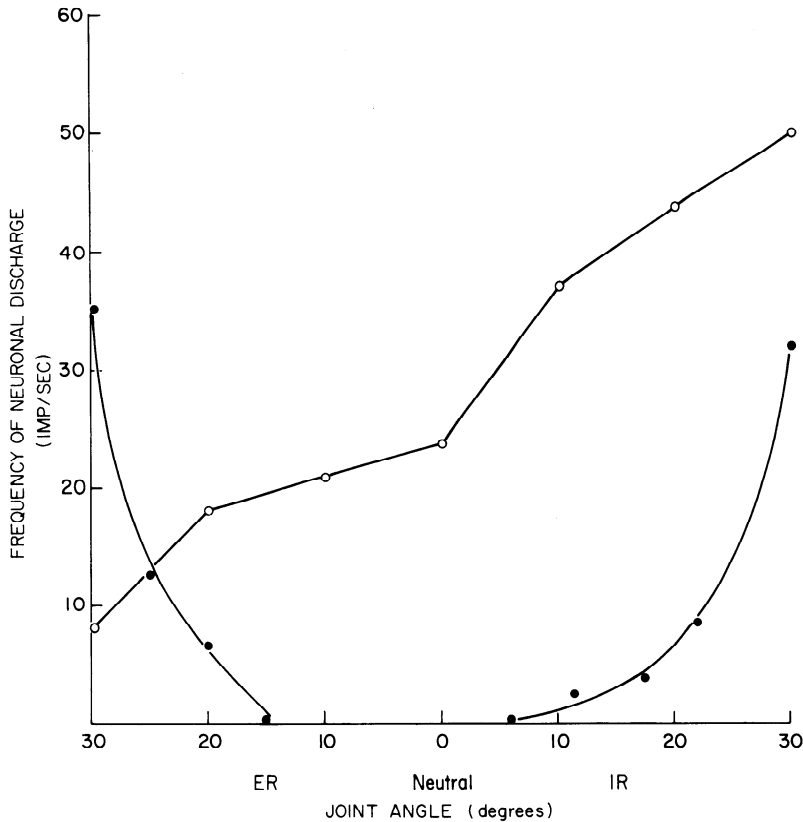


FIG. 13. Response of an identified afferent from the GI muscle (open circles), using axial rotation of the femur. Included for comparison are two capsule afferents (filled circles): one (left side) is from the anterior capsule, sensitive to external rotation, and one (right side) is from the posterior capsule, sensitive to internal rotation.

five afferents that responded to IR and for which we measured thresholds had a mean threshold of 11° . This is not different from thresholds in the entire population (see Fig. 6). Thus we conclude that the presence or absence of muscles around the hip does not significantly alter the properties of receptors that reside in the capsule.

Conduction velocities

Conduction-velocity measurements were made on 67 capsule afferents. Conduction velocities ranged from 12 to 96 m/s, with a modal value of 42 m/s.

Comparison of properties of capsule afferents to properties of gemellus inferior muscle

The properties of capsule afferents described in this paper are very different from those of the afferents described by Carli et

al. (5). In an attempt to reconcile the two sets of observations, we present here evidence that suggests that the full range neurons described by Carli et al. (5) are in fact afferents from the gemellus inferior (GI) muscle. In three experiments we replicated the experimental preparation of Carli et al. (5). This differs from our preparation in that Carli et al. (5) did not denervate or remove the GI muscle, whose axons run in the QF nerve along with fibers of the hip PAN. The results from these experiments are presented here in order to show the similarity of the properties of GI afferents to the full range afferents of Carli et al. (5). Figure 13 shows the discharge of one GI afferent plotted versus joint angle in axial rotation. As may be seen, this is a full-range afferent whose discharge increases as the femur is rotated into internal rotation. Included for comparison



FIG. 14. Response of the full-range afferent shown (open circles) in Fig. 13, observed during contraction of the GI muscle while the femur was fixed in the hip rotator stimulator. The joint did not rotate visibly during the twitch. Lower trace shows axial torque (g-cm) recorded during twitch.

are recordings of two capsule afferents, one each from the anterior and posterior capsule. The muscle afferent is exactly analogous to the results of Carli et al. (Fig. 7 of Ref. 5). The afferent that we present in Fig. 13 was a muscle afferent: it responded vigorously to SCH administration, it had a conduction velocity of 100 m/s, and it responded to tugging or palpating the GI muscle. Furthermore, as shown in Fig. 14, its discharge paused on contraction of the GI muscle. Twelve GI afferents so studied were similar to the above: sensitivities were different but the properties were not qualitatively different between neurons. Like the full range receptors described by Carli et al., all our gemellus inferior afferents were active at all joint positions and maximally excited by internal rotation and adduction.

Conduction velocity of gemellus afferents ranged from 50 to 111 m/s, with a modal value of 100 m/s.

DISCUSSION

The most important aspect of these results is that all of the slowly adapting afferents from the hip capsule discharge only when the joint is rotated into its limit of movement. Furthermore, the stimulus to which an afferent is sensitive is determined in a logical

fashion by the geometry of the joint and the location of the receptor in the capsule. A given receptor responds only to that rotation that would load the region of the capsule where the receptor resides. No other rotations excite the afferent. This is a greatly simplifying concept in understanding the function such receptors might have, since when the hip is rotated into a limit of its movement along some axis, activity is evoked only in a fraction of the total population of receptors. Thus when the hip is rotated toward a limit, hip position is signaled with great specificity. The axis of the rotation is signaled by the subpopulation responding, and the extent of the movement is signaled by the frequency of afferent discharge. It is important to note that all positions of the femur are not encoded by discharge in capsule afferents: neutral or intermediate positions of the hip, in which the capsule is not loaded, do not result in activity in capsule afferents. Thus in the hip as in other joints, capsule receptors may be considered as limit detectors. Furthermore, flexion and extension movements are not signaled by capsule afferents. It should be noted that the flexion and extension rotations that we employed were limited by the resulting movements of the spinal cord to angles between 45° (flexion) and 140° (extension). Since flexion and extension produce torsion in the capsule, continued flexion or extension should ultimately activate capsule receptors. However, we wish to point out that the flexion and extension movements that we used are clearly greater than the range of excursions observed in normal movements in cats (14), so that hip afferents would make no contribution to position sense in normal flexion or extension movements. Furthermore while the extent of normal abductive or axial rotations have not been described in cats, we note that the range of axial rotations observed in the human hip during normal walking (20, 24) is about 4° ER and 4° IR, so that hip afferents would be quite unlikely to contribute to axial position sense.

When describing afferent responses in relation to rotations of the joint into limits of movement, there is the possibility that the stimuli employed may be noxious. We note however that our rotations are in all cases

less than the published descriptions of the limits of rotation in the human hip (1). Furthermore, the stability of responses observed in afferents recorded for long periods of time also suggests that the systems we studied were not injured or damaged.

It has been proposed, based on results from the knee joint, that posterior capsule receptors are load- or stretch-sensitive afferents (16, 18), which are excited by capsule loading in extreme rotations. This model is consistent with findings from all the freely moving joints (4, 16, 22, 27) that have been previously studied; we now show that it is consistent also with the hip joint. Results from costovertebral joints (14) are different from the above: receptors from this joint respond throughout the entire range of angles of the joint. However, we wish to point out that this is not a freely moving articulation like the joints of limbs, and the mechanics of the capsule of such a joint could be different than the mechanics of a mobile, freely moving limb joint.

With regard to the specific relationship between capsule load and neuronal discharge, it is not possible in this paper to quantify the relationship between capsule load and response in more than a general way. In the hip, the torque produced by rotating the joint results from stretching a host of structures in addition to the capsule. Thus the value of torque used to characterize afferents in our results should not be taken as more than a general index of capsule load.

The variability in the properties (e.g., thresholds and sensitivities) of individual afferents probably reflects the properties of afferents in different capsule locations, studied in relation to a single standard stimulus (internal or external rotation). Furthermore, we have made the simplifying assumption that the capsule is a uniform structure. The presence of any inhomogeneities such as capsule thickenings would result in nonuniform strain distributions and would therefore result in different characteristics in different neurons.

Our results are, of course, sharply divergent from those of Carli et al. (5), and we wish to stress that when we replicated the conditions of their experiment, we obtained recordings of afferents from the GI muscle

that were very similar to their results. The presence of large numbers of muscle afferents in the nerve they recorded from would, by virtue of sampling probabilities, result in the recording of muscle afferents. When we replicated their experimental protocol, we sampled 12 GI afferents and 1 capsule afferent in three experiments. Furthermore, since they left the GI muscle intact in their preparation, there was no way to stimulate the capsule surface directly and verify the origin of afferents. Thus we believe that the results of Carli et al. (5) can be considered to be recordings of GI afferents (with the exception of three limited-range afferents that are similar to our capsule afferents). In another publication, Carli et al. (7) reported that "joint" afferents had different properties than muscle (gluteus medius) afferents. Position sensitivity of afferents, studied using axial rotations and ab- and adduction, was different between these two types of afferents. Joint afferents had higher sensitivity to both axial and abductive-adductive rotations. However, we wish to point out that such differences do not mean that both sets of afferents cannot be muscle afferents. The position sensitivity of GI afferents would be expected to be different from that of gluteus medius afferents on the basis of differences in orientation, insertions, and dimensions of the muscles. The gluteus medius is an abductor of the femur, which would be optimally stretched with adductions, and the GI is an external rotator, which would be maximally stretched with internal rotations. Comparing the responses would naturally result in different sensitivity for GI afferents than gluteus medius afferents.

In conclusion, we wish to restate a general model for activation of capsule afferents. Capsule receptors act like stretch receptors, and their response can be interpreted in terms of stretching of joint tissues resulting from angular displacement of the joint. In freely moving joints, the angles at which the capsule is loaded and capsule afferents are activated are at the limit of movement of the joint. In this way, capsule receptors act like limit detectors. Within the range of their activation, they are able to encode the axis of joint rotation and the extent of rotation with great specificity.

ACKNOWLEDGMENTS

We gratefully acknowledge the assistance of Cyril Rodgers who built the hip rotator and of Kevin E. Fogarty for writing computer programs.

This work was supported by National Institutes of Health Grant NS-10783.

Received 25 September 1981; accepted in final form 5 January 1982.

REFERENCES

1. BOONE, D. C. AND AZEN, S. P. Normal range of motion of joints in male subjects. *J. Bone Jt. Surg. Am. Vol.* 61: 756-759, 1979.
2. BOYD, I. A. AND ROBERTS, T. D. M. Proprioceptive discharges from stretch-receptors in the knee joint of the cat. *J. Physiol. London* 122: 38-58, 1953.
3. BRANTIGAN, O. C. AND VOSHELL, A. F. The mechanics of the ligaments and menisci of the knee joint. *J. Bone Jt. Surg.* 23: 44-66, 1941.
4. BURGESS, P. R. AND CLARK, F. J. Characteristics of knee joint receptors in the cat. *J. Physiol. London* 203: 317-335, 1969.
5. CARLI, G., FARABOLLINI, F., FONTANI, G., AND MEUCCI, M. Slowly adapting receptors in cat hip joint. *J. Neurophysiol.* 42: 767-779, 1979.
6. CARLI, G., FONTANI, G., GRIGG, P., AND ROSSI, A. Proprieta dei recettori articolari dell'anca di gatto studiate dopo taglio del muscolo gemello inferiore e nella capsula isolata. *Atti Soc. Ital. Fisiol. Caserta* 2-4 Ott. 133, 1980.
7. CARLI, G., FONTANI, G., AND MEUCCI, M. Static characteristics of muscle afferents from gluteus medius muscle: comparison with joint afferents of hip in cats. *J. Neurophysiol.* 45: 1085-1095, 1981.
8. CLARK, F. J. Information signaled by sensory fibers in medial articular nerve. *J. Neurophysiol.* 3: 101-110, 1972.
9. CLARK, F. J. AND BURGESS, P. R. Slowly adapting receptors in cat knee joint: can they signal joint angle? *J. Neurophysiol.* 38: 1448-1473, 1975.
10. CROUCH, J. E. *Atlas of Cat Anatomy*. Philadelphia: Lea & Febiger, 1969.
11. CROWNSHIELD, R., POPE, M. H., AND JOHNSON, R. J. An analytical model of the knee. *J. Biomech.* 9: 397-405, 1976.
12. DEE, R. Structure and function of hip joint innervation. *Ann. R. Coll. Surg. Engl.* 45: 357-374, 1969.
13. ELDRED, E., SCHNITZLEIN, H. N., AND BUCHWALD, J. Responses of muscle spindles to stimulation of the sympathetic trunk. *Exp. Neurol.* 2: 13-25, 1960.
14. GODWIN-AUSTEN, R. B. The mechanoreceptors of costovertebral joint. *J. Physiol. London* 202: 737-753, 1969.
15. GOSLOW, G. E., REINKING, R. M., AND STUART, D. G. The cat step cycle: hind limb joint angles and muscle lengths during unrestrained locomotion. *J. Morphol.* 141: 1-41, 1973.
16. GRIGG, P. Mechanical factors influencing response of joint afferent neurons from cat knee. *J. Neurophysiol.* 38: 1473-1484, 1975.
17. GRIGG, P., FINERMAN, G. A., AND RILEY, L. H. Joint position sense after total hip replacement. *J. Bone Jt. Surg. Am. Vol.* 55: 1016-1025, 1973.
18. GRIGG, P. AND HOFFMAN, A. H. Properties of Ruffini afferents revealed by stress analysis of isolated sections of cat knee capsule. *J. Neurophysiol.* 47: 41-54, 1982.
19. GRIGG, P., HOFFMAN, A. H., AND FOGARTY, K. E. Properties of Golgi-Mazzoni afferents in cat knee joint capsule, as revealed by mechanical studies of isolated joint capsule. *J. Neurophysiol.* 47: 31-40, 1982.
20. JOHNSON, R. C. AND SMIDT, G. Measurement of hip-joint motion during walking. *J. Bone Jt. Surg. Am. Vol.* 51: 1083-1094, 1969.
21. MILLAR, J. Joint afferent fibres responding to muscle stretch, vibration and contraction. *Brain Res.* 63: 380-383, 1973.
22. MILLAR, J. Flexion-extension sensitivity of elbow joint afferents in cat. *Exp. Brain Res.* 24: 209-214, 1975.
23. O'CONNELL, R. J., KOCIS, W. A., AND SCHOENFELD, R. L. Minicomputer identification and timing of nerve impulses in a single recording channel. *Proc. IEEE* 61: 1615-1621, 1973.
24. SAUNDERS, J. B. DE C., M., INMAN, V. T., AND EBERHART, H. D. The major determinants in normal and pathological gait. *J. Bone Jt. Surg. Am. Vol.* 35: 543-558, 1953.
25. SKOGLUND, S. Anatomical and physiological studies of knee joint innervation in the cat. *Acta Physiol. Scand.* 36, Suppl. 124: 1-101, 1956.
26. SMITH, C. M. Neuromuscular pharmacology: drugs and muscle spindles. *Ann. Rev. Pharmacol.* 3: 223-224, 1963.
27. TRACEY, D. J. Characteristics of wrist joint receptors in the cat. *Exp. Brain Res.* 34: 165-176, 1979.
28. WISMANS, J., VELDPAUS, F., JANSEN, J., HUSON, A., AND STRUBEN, P. A three-dimensional mathematical model of the knee joint. *J. Biomech.* 13: 677-685, 1980.