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## Somatosensory unit input to the spinal cord during normal walking

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Chronic recording techniques in freely walking cats have been used to sample unitary activity from most large myelinated afferent classes. Cutaneous mechanoreceptors are highly sensitive and generate regular activity patterns predictable from their modalities. Knee joint afferents can fire briskly during midrange locomotory movements but appear to be influenced by factors other than joint angle. Golgi tendon organs generate activity consistent with sensitivity to active muscle tension. Muscle spindle afferents do not appear to conform to any single functional pattern for all muscles. It is suggested that degree and rate of stretch are sensed by spindles (possibly under dynamic fusimotor bias) in extensor muscles which normally undergo isometric or lengthening contractions whereas rapidly modulated static fusimotor activity is employed to preserve spindle activity during the rapidly shortening contractions of flexor muscles. Both patterns may be represented in different spindles of bifunctional, biarticular muscles such as rectus femoris and sartorius.

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Des techniques d'enregistrement chronique ont été utilisées pour recueillir l'activité unitaire de la plupart des classes de grosses fibres afférentes chez le chat qui marche librement. Les mécanorécepteurs cutanés sont très sensibles et génèrent une activité régulière qui peut être prédite d'après leur modalité sensorielle. Les afférences articulaires du genou peuvent décharger intensément au cours du mouvement locomoteur à des positions articulaires intermédiaires mais apparaissent influencées par des facteurs autres que l'angle articulaire. Les organes tendineux de Golgi génèrent une activité compatible avec leur sensibilité à la tension musculaire activée. Les afférences des fuseaux neuromusculaires ne se conforment pas apparemment à un modèle unique pour tous les muscles. Il est suggéré que le montant et le taux d'étirement sont détectés par les fuseaux (possiblement sous une influence fusimotrice dynamique) dans les muscles extenseurs qui normalement se contractent de façon isométrique ou avec un allongement alors que l'activité fusimotrice statique qui a une modulation rapide est employée pour préserver l'activité fusoriale pendant les contractions rapides avec raccourcissement des muscles fléchisseurs. Ces deux modes peuvent être représentés dans des fuseaux différents de muscles biarticulaires et bifonctionnels tels le rectus femoris et le sartorius.

Over the past half century, the application of single unit recording techniques has provided extensive information about the mechanical properties of the various specialized mechanoreceptors of the limb. Although differing classification schemes have been proposed, there is general agreement on the major divisions, particularly for the larger myelinated fibers whose conduction velocities would allow them to play an important role in rapid motor control and compensation (Matthews 1972; Burgess et al. 1968; Horch et al. 1977). However, for many modalities it is difficult to extrapolate from the receptor sensitivity data obtained with controlled probing in reduced preparations to the actual activity that would occur during normal use of the limb. This is particularly true for those receptors which interact directly with voluntary muscle activity, i.e., spindles, tendon organs, and joint stretch receptors.

This review will discuss recent and still somewhat sketchy data on somatosensory activity from normally moving limbs as observed in intact animals using newly developed techniques for chronic unit recording.

Severin et al. (1967) presented the first data on muscle receptors in the moving limb during locomotory movements elicited in decerebrate cats by tonic stimulation of what has become known as the midbrain locomotory center. The unit records presented here and elsewhere (Loeb et al. 1977; Loeb and Duysens 1979) from this laboratory have been obtained from intact, freely moving cats using a floating fine wire electrode array in cat dorsal root ganglia (L5, L7, S1 levels); the technique has been described previously (Loeb et al. 1977; Loeb and Duysens 1979). Various kinesiological parameters are recorded along with these microelectrode signals to try to identify the mechanical factors, intrinsic and extrinsic to the body, which have contributed to the observed activity. Records have included videotape for single field (60 field per second) analysis, electromyograms (EMG) from surgically implanted bipolar electrodes, and muscle length or joint angle from implanted length gauges (Loeb et al. 1980). More recently, techniques have been developed for continuous measurement of single tendon strain (Walmsley et al. 1978) and foot fall timing (Chapin et al. 1980) but these have not

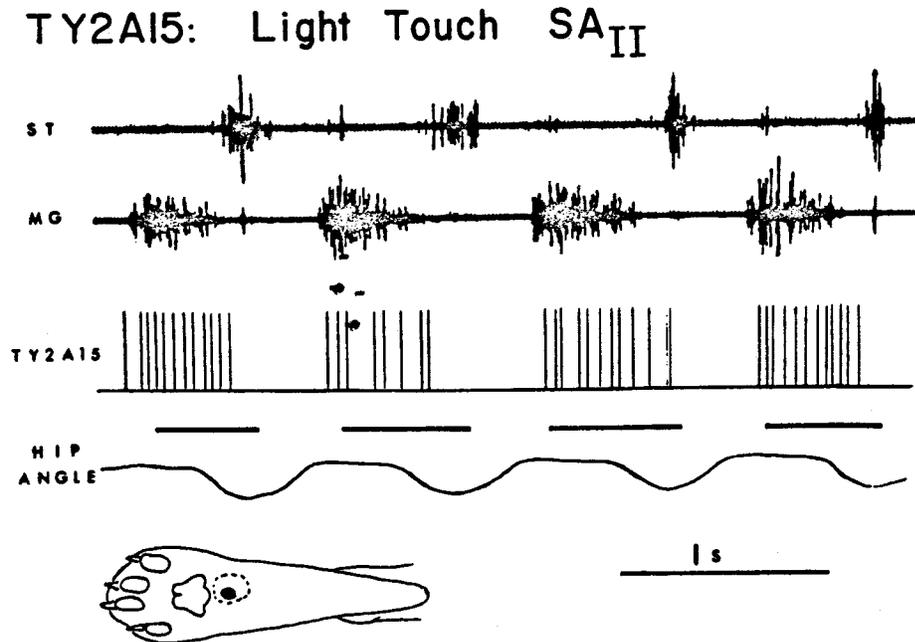


FIG. 1. The activity of a slowly adapting, stretch-sensitive cutaneous mechanoreceptor during four normal walking step cycles. ST (semitendinosus) and MG (medial gastrocnemius) EMG for reference; interrupted horizontal line indicates stance phase (foot contact observed on videotape), hip angle from implanted length gauge. Unit firing shown as acceptance pulses from window discriminator (Bak Electronics DIS-1). Dotted line surrounding darkly hatched receptor field indicates approximate area of skin stretch sensitivity.

yet been systematically employed in chronic afferent unit recording.

Similar microelectrode and kinesiological techniques have been employed by Arthur Prochazka and his colleagues to record from large myelinated afferent fibers in the dorsal roots of the L6, L7, and S1 segments in freely walking cats (Prochazka et al. 1976, 1977; Prochazka et al. 1979). Pertinent data from spindle afferents from human ankle muscles during standing and controlled voluntary movements have been obtained by David Burke and colleagues (recently reviewed by Burke 1981) using the technique of Vallbo (1970) for percutaneous insertion of single, tapered, rigid metal microelectrodes into peripheral nerve.

#### Cutaneous mechanoreceptors

Most chronic recording attempts have concentrated on the proprioceptive afferents but cutaneous receptors have, in our experience, been the larger, more numerous, and more easily identified units recorded. They are easily separated into two groups: (a) rapidly adapting receptors activated by very small movements of one or a few hairs and (b) low threshold receptors with small fields requiring direct skin deformation. Conduction velocity, usually obtained by electrical stimulation of the apparent location of the receptor ending, permits

some further segregation of hair receptors into the G<sub>1</sub>, G<sub>2</sub>, and D categories of Burgess et al. (1968). The slowly adapting, low threshold skin receptors are easily segregated into SA<sub>I</sub> and SA<sub>II</sub> categories on the basis of their responsiveness to skin stretch in addition to direct vertical deformation. Finer distinctions and identification of rarer receptor types has seemed unwarranted because of the considerable heterogeneity of sites being compared (proximal versus distal, underlying bone, glabrous pad skin, proximity to claws, etc.) which could influence the expression of receptor properties and responses to our manipulations.

Although we have recorded from well over 200 cutaneous afferents, we have examined in detail perhaps a dozen during locomotion, intentionally looking for unusual patterns. For the most part cutaneous receptors behaved as might be expected, particularly from more proximal skin sites. Direct contact between the receptive field and any object generally activated most low threshold mechanoreceptors. Stretch-sensitive receptors and hair receptors located near folds in the skin were activated by the normally occurring sliding and folding motion of the skin during walking. An example of such sensitivity in an SA<sub>II</sub> receptor in noncontacted skin is shown in Fig. 1. Note that the skin stretch during the E<sub>1</sub> phase preceding foot fall was presumably the

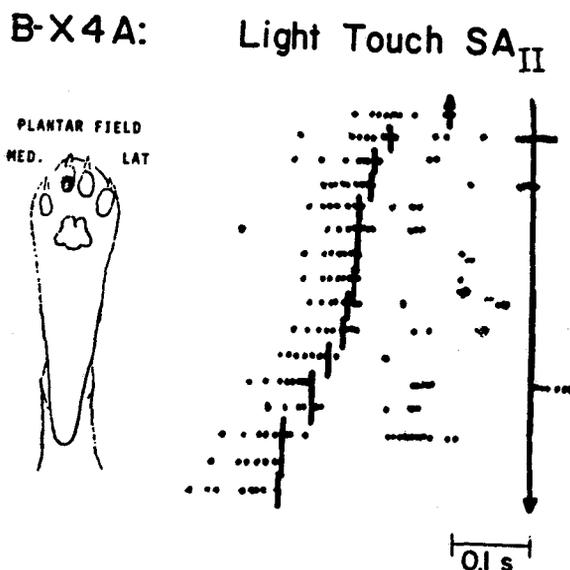


FIG. 2. Activity of a slowly adapting, stretch-sensitive cutaneous mechanoreceptor from posterior half of second toe pad. Selected step sequences rastered in order of increasing swing phase duration, centered on foot fall; dots indicate unit firing and short vertical lines indicate foot lift-off as observed from videotape.

effective stimulus and there was no particular response to any sudden "shock wave" at foot fall. Responses of two hair receptors from the distal foot have been published elsewhere (Loeb et al. 1977), showing a similar activation during  $E_1$  toe movements for one of them. These records suggest some caution in interpreting activity of higher order cells (e.g., in sensory or motor cortex) as "anticipating" expected skin contact before the assumed onset of cutaneous receptor activation.

Most of our cutaneous receptor records show a remarkable uniformity of firing pattern from step to step despite the very small perturbations which must be responsible for activation of the endings. This may be contrasted with the responses to sensory input of higher order integrative neurons, which often require averaging or histogramming for the response patterns to emerge clearly. It is shown in Fig. 2 that the receptor sensitivity can, apparently, respond to modulations in performance not visible on a film record of the task. A series of step cycles has been rastered around the occurrence of foot fall and arranged in increasing duration (slower gait). At foot lift, there is a stereotyped response of the slowly adapting receptor (located in one toe pad) regardless of speed of gait. However, there are occasional distinct bursts during midswing and (or) at foot fall which are unrelated to speed or other visible aspects of the locomotion. We can only guess that some subtle difference between step cycles in fact occurred.

One possibility is a change in the degree of claw extension as the distal phalanx, to which the claw is fixed, rotated through the fleshy mass of the pad in which the receptor was located. Interestingly, we have noted in other animals a prominent but very variable EMG burst from flexor digitorum longus, the claw extending muscle, just after foot lift.

### Joint receptors

The role of joint receptors in providing our sense of limb position has been much debated over the past several decades (Boyd and Roberts 1953; Skoglund 1956; Millar 1973; Clark and Burgess 1975; Grigg and Greenspan 1977; Ferrell 1980). Most electrophysiological studies are based on data from the posterior articular nerve of the knee joint in anesthetized, immobile cats. Two questions remain open. First, is there a reasonable population of receptors which are activated during the midrange joint angles that normally occur during locomotion or are the receptors primarily responsive only to extreme movements involving non-physiological stresses or torque directions (hence, functioning as nociceptors)? Second, is receptor activity closely correlated with joint angle or are other factors such as vertical loading and strain via capsular muscle insertions modulating the firing rate and "contaminating" the joint angle data?

We have recorded from eight units which we believed were knee joint receptors based on limb manipulation, local application of vibratory stimuli, and percutaneous electrical activation. Several of these were activated only by axial rotations rather than flexion-extension and fired only rarely during locomotion. Two units with interesting activity patterns were more extensively studied, including acute dissection to identify their nerve of origin. These two were confirmed to be from the posterior articular nerve by direct electrical stimulation of that nerve with hook electrodes in oil and, for one unit, by spike-triggered averaging of the appropriately delayed neurogram recorded from the hooks during physiological activation as shown in Fig. 3. A record of the unit activity during walking for the other unit (from the same animal) has been published elsewhere (Loeb et al. 1977) and showed considerably higher rates of firing but a similar pattern. Only ankle angle recordings were available but our experience suggests that knee angle trajectories can be reliably inferred from them for slow, unperturbed walking (see Fig. 5). Basically, both knee and ankle angles are relatively constant throughout stance, with some flexion yielding near the beginning and some extra extension at the end. The range of movement is much larger during the swing phase, with both joints progressing rapidly first to the maximum flexion encount-

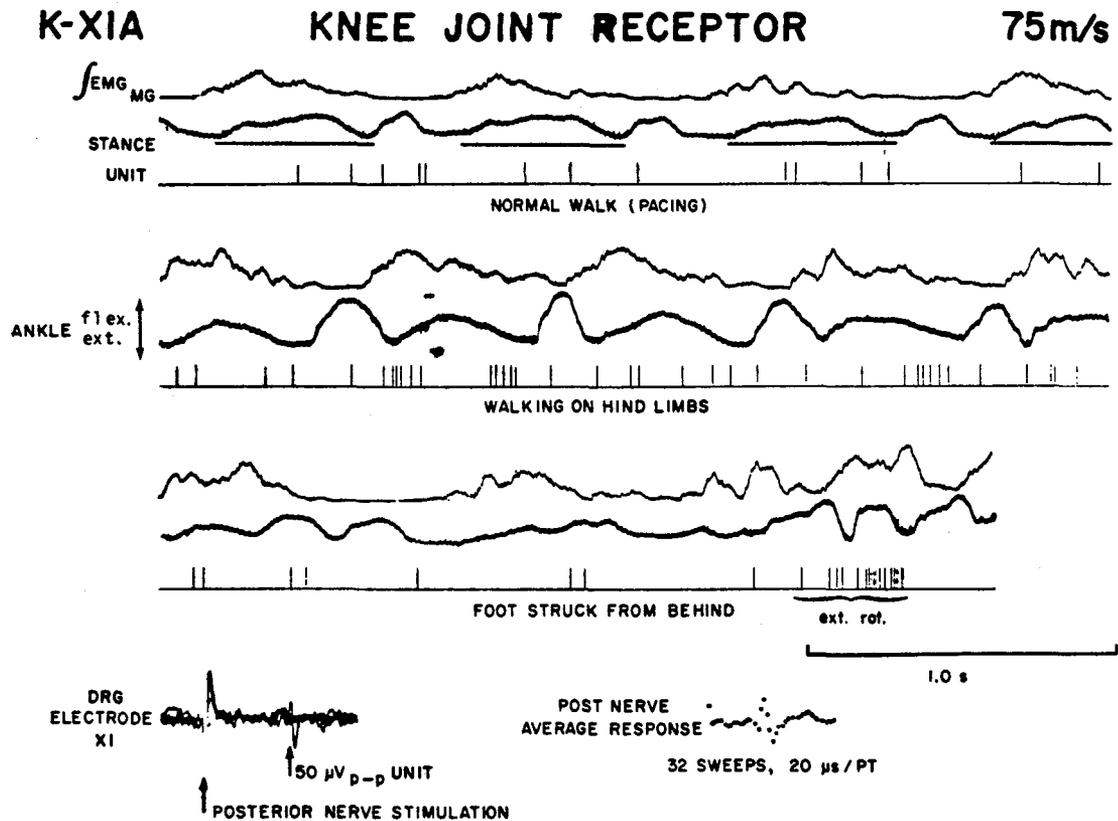


FIG. 3. Activity of a knee joint receptor during normal and perturbed locomotion. Paynter filtered EMG (Bak Electronics PF-1) from MG (medial gastrocnemius muscle) and ankle angle from implanted length gauge for reference; interrupted horizontal lines indicate stance phase from videotape. Inserts at bottom show (left) method of determining 75 m/s conduction velocity by electrically stimulating exposed posterior articular nerve (50  $\mu$ s pulse, three superimposed traces at 1.08 times threshold, 5 ms long) and (right) confirmation of origin using physiologically evoked dorsal root ganglion spike activity to trigger a signal averager looking at a delayed signal from the whole nerve recorded by bipolar nerve hooks in mineral oil. Latency to electrical stimulation at 2 times threshold was 2.0 ms with 151-mm conduction distance measured at postmortem dissection. Latency of spike-triggered average neurogram was  $-2.16$  ms after correcting for delay.

ered, then to the maximum extension just prior to foot contact. Both units had most of their activity during the stance phase and less activity during the larger angular changes of the swing phase. The unit in Fig. 3 was further activated by the increased loading of the joint caused by the cat placing his forepaws on a stationary raised platform and walking only with his hind legs. A particularly vigorous burst occurred after he brushed against a backstop in the treadmill and made a voluntary escape maneuver that included an outward turning of the foot. Passive manipulation under anesthesia (but before joint dissection) confirmed that this unit was very sensitive to such small outward rotations, which seemed unlikely to be perceived as noxious. A previously discussed consideration that these units might be popliteus muscle spindles (Burgess and Clark 1969) now appears to be dismissable based on more recent data (Ferrell 1980).

Based on this very limited experience, we think we can support the recent acute study of Ferrell (1980) which rekindles the notion that the joint receptors can fire at the midrange joint angles. On the other hand, we would agree with the view put forward by Grigg and Greenspan (1977) that factors other than joint angle can significantly influence the receptors, thus making the sense of limb position dependent on more complex signal processing than simple readout of the joint receptor activity.

#### Golgi tendon organs

There is general agreement that the factors influencing the Golgi tendon organ (GTO) receptor are limited to the tensions of the tendinous filaments arising from the particular muscle fibers around which a given afferent ending is entwined (Matthews 1972; Schoultz and Swett 1972). There is less agreement about the linearity

with which the various tensions combine to produce a given rate of receptor firing (Stuart and Stephens 1976; Jami and Petit 1976; Gregory and Proske 1979).

The activity of three chronically recorded GTO's is shown in Fig. 4 along with unprocessed and integrated EMG traces from synergistic muscles during normal walking. Unfortunately, we have no records in which the source of the chronically recorded EMG and the location of the GTO (identified by manipulation and electrical stimulation) were identical. The identification of receptor modality was based on their relative insensitivity to muscle stretch during deep anesthesia (pentobarbital and (or) ketamine) and their ready activation by electrically induced contraction of the parent muscle (via percutaneously inserted needle electrodes) and by reflex withdrawal contractions to noxious stimuli during light anesthesia. In contrast, muscle spindle afferents (discussed below) were always sensitive to muscle stretch even during deep pentobarbital anesthesia and were seen to pause during electrically induced twitch contractions of their parent muscles. Although anomalous responses can be obtained from both receptor modalities with excessive or improperly localized electrical stimulation, careful probing with a vibrator coupled with appropriately directed passive manipulation during anesthesia was quite unambiguous.

The activity of the GTO from medial gastrocnemius (Fig. 4A) suggests a close correlation with the general timing of the parent muscle activity but little tendency to follow the short-term irregularities in EMG amplitude which are characteristic of both medial and lateral gastrocnemius. This activity would, however, be consistent with a GTO dominated by tension in slow motor units, which are likely to be recruited throughout the active tension period and fluctuate little in their tension output (see Walmsley et al. 1978; also unpublished records from slow knee extensor motor neurons during walking).

A more rapidly modulated response in tibialis posterior, which is generally synergistic with the triceps surae group, is suggested in Fig. 4B. The varying level of effort for these three steps evidenced by the EMG in the medial gastrocnemius is reflected in the overall activity of the afferent. The large, sudden changes in firing rate suggest either influence from one or more unfused fast twitch units or possibly occlusion from conflicting pacemaker sites as recently demonstrated by Fukami (1980).

Only a very low and intermittent firing rate during stance for a GTO in flexor digitorum brevis is shown in Fig. 4C. This is consistent with recent EMG recordings we have made from this muscle during normal walking showing irregular recruitment of a small number of units throughout the stance phase (Abraham and Loeb, unpublished data).

In summary, our interpretation of the available GTO firing patterns says more about the limited state of knowledge about whole muscle utilization and motor unit recruitment patterns than about receptor function.

### Muscle spindles

The spindle afferents are generally viewed as playing some important role in motor control and, less certainly, in our sense of kinesthesia (reviewed by Roland 1978), consistent with their fast conduction velocity and highly sensitive and specialized receptor organ. However, the magnitude and even the nature of their sensitivity is dominated by a complex active internal structure of at least three kinds of muscle fibers with two kinds of motor innervation which have input pathways suggesting afferent reflexes and segmental and descending modulation (see review by Murthy 1978).

Direct observation of fusimotor activity during normal motor behavior is technically very difficult and has been limited to the respiratory system (Andersen and Sears 1970), the jaw muscles (Appenteng et al. 1979; Taylor et al. 1981), and lightly anesthetized preparations (Gildenberg and Murthy 1977). Generally, fusimotor activity has had to be inferred from spindle afferent activity by looking for deviations in afferent activity from known or presumed responsiveness to similar movements under deafferented (deeply anesthetized) conditions.

The three groups currently looking at spindle afferent activity during normal limb movements have arrived at three different conclusions, which can be stated (and undoubtedly oversimplified) as follows. From human microneurography during controlled movements, Hagbarth and Vallbo (1968) and Burke (1981) have concluded that fusimotor contractions dominate muscle spindle firing and that fusimotor activity is always linked in fixed proportion to extrafusal activity (a concept known as  $\alpha$ - $\gamma$  coactivation). From recordings of lumbosacral dorsal root units in walking cats, Prochazka et al. (1979) have concluded that fusimotor coactivation dominates spindle firing only for low velocity contractions but that this factor is absent or inadequate to compensate for active or passive length changes faster than 0.2 muscle rest lengths per second. From a similar preparation, we, unfortunately, draw conclusions quite unlike either. We stand by our original, limited conclusion that during voluntary, unperturbed behavior (involving extrafusally active muscles either shortening or lengthening at any rate), the fusimotor system is activated so as to maintain a moderate rate of afferent discharge which may then be modulated up or down by the kinematic details of the movement (Loeb and Duysens 1979). The apparent differences in interpretation appear to arise from the very different motor tasks performed by different muscles as

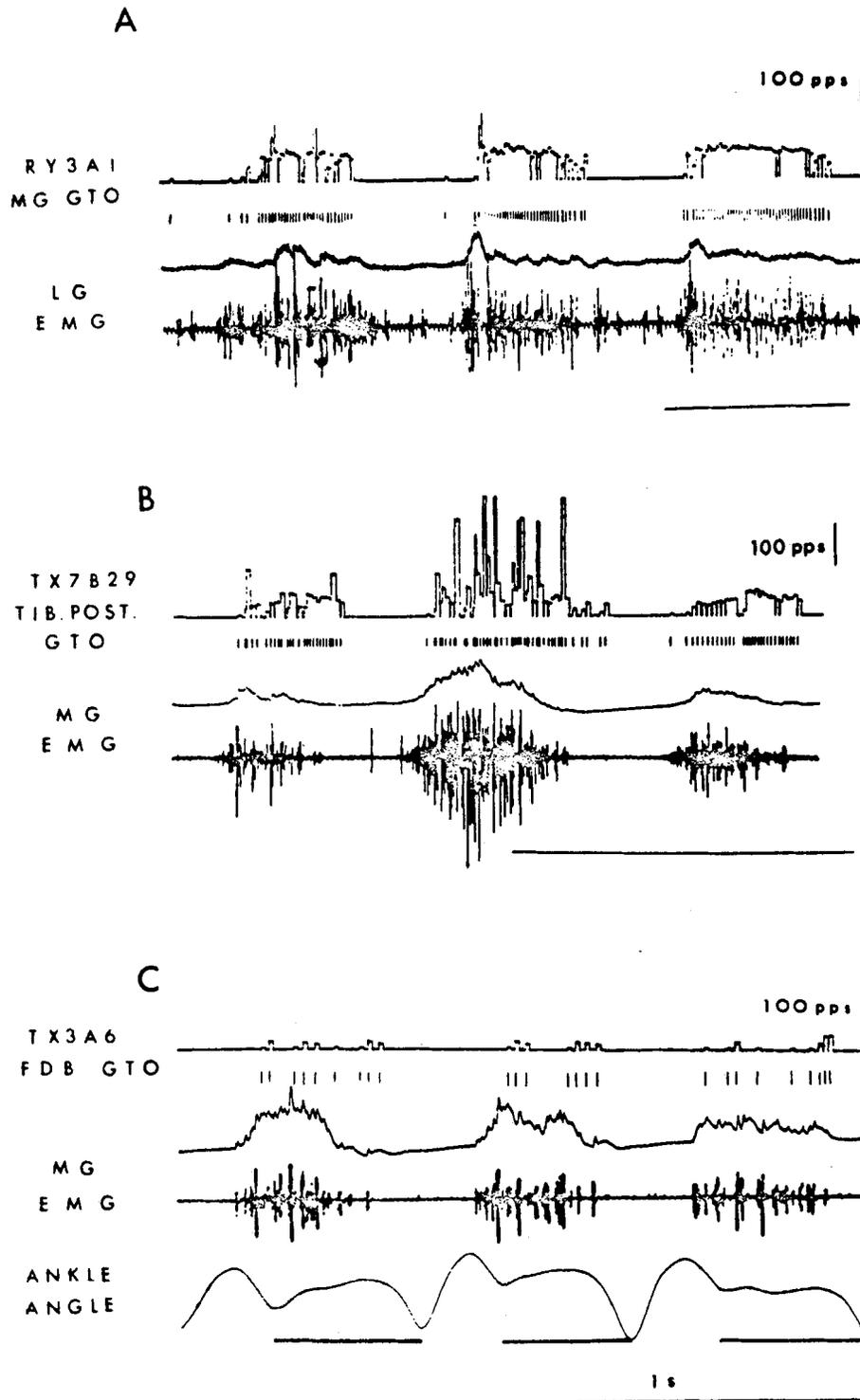


FIG. 4. Activity of three Golgi tendon organ receptors from medial gastrocnemius (A, MG GTO), tibialis posterior (B, Tib. Post.), and flexor digitorum brevis (C, FDB GTO) muscles. Top two traces in each show unit firing as frequency in spikes per second and as discriminated pulses; bottom two traces show Paynter filtered (50 ms time constant) and raw EMG from synergistic muscles.

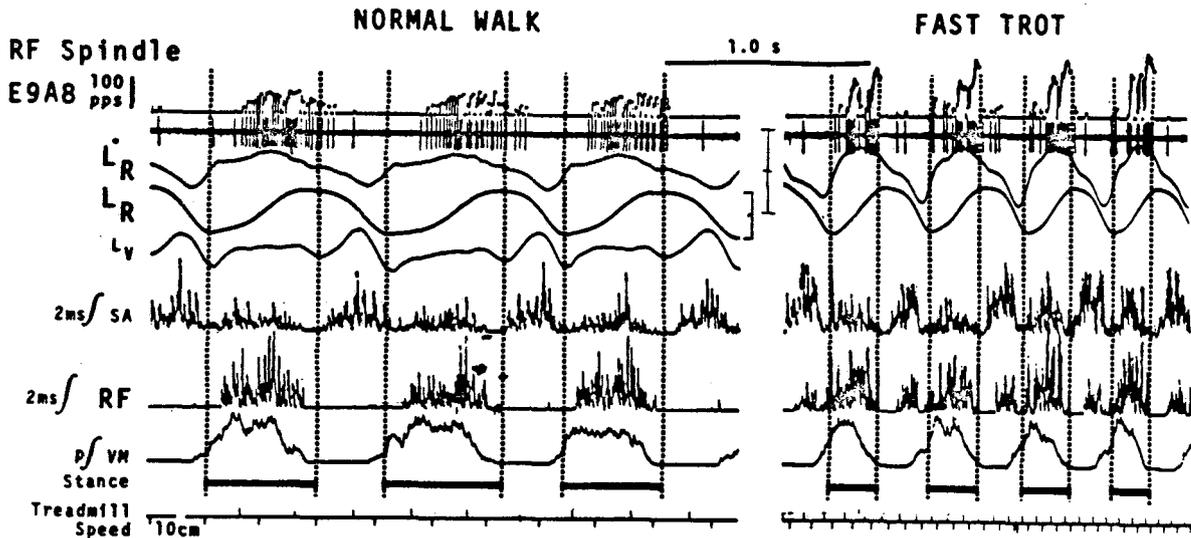


FIG. 5. Activity of a muscle spindle afferent from rectus femoris (RF) muscle during unperturbed walk and trot. Traces from bottom up are as follows: treadmill speed timing pulses; foot contact as observed on videotape; Paynter filtered EMG from vastus medialis (VM), a pure knee extensor; pulse integrated EMG (2 ms bins (Bak and Loeb 1979)) from RF; pulse integrated EMG from sartorius; length of vastus muscles (stretch upwards, omitted during trot); length of rectus-sartorius muscles (from implanted length gauges); electronic time derivative of rectus-sartorius length giving velocity; raw microelectrode signal; unit activity in spikes per second. Length calibration (from cadaver dissection duplicating joint angles) shows RF walking excursion from 82 to 92 mm (rest length 87 mm); velocity calibration  $\pm 1.0$  rest length per second.

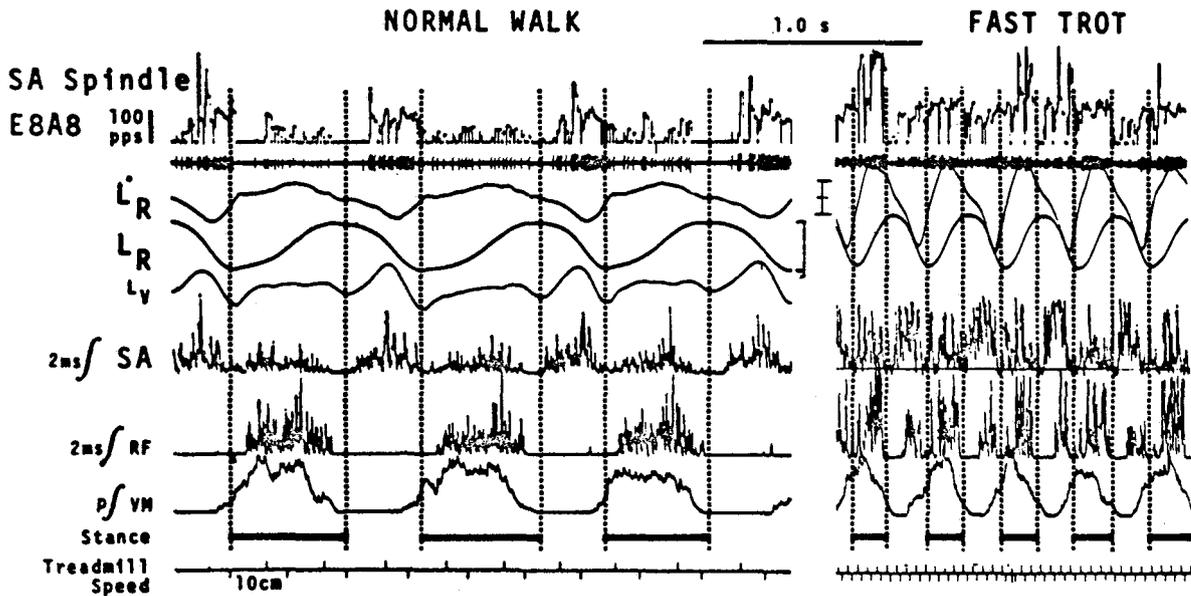


FIG. 6. Activity of a muscle spindle afferent from sartorius (SA) muscle; traces as in Fig. 5. Length calibration shows SA (extensor part) normal walking excursion from 103 to 127 mm (rest length 101 mm); velocity calibration  $\pm 1.0$  rest length per second.

they are observed by different investigators. During locomotion, the work of the extensor and flexor muscles is quite different. Flexors generate rapid, unopposed shortening contractions during which

a passive (defferented) spindle would almost certainly be completely unloaded and silent. Extensors generally yield (i.e., lengthen), at least at the beginning of their active phase. This springlike property results in nega-

tive work which is recovered during the propulsive shortening of the late stance phase. Spindles in such muscles should be synergistically activated by both the extrinsic lengthening and whatever fusimotor "coactivation" accompanies the extrafusal contraction. We and others have previously presented data which demonstrate that spindle firing during locomotion is neither particularly high during the active lengthening of extensors (Prochazka et al. 1976, 1977) nor abolished by the shortening contraction of flexors (Loeb and Duysens 1979). A similar dichotomy was noted by Feldman et al. (1977) for the same muscles during scratching, where both extensors and flexors actively shorten: tibialis anterior (flexor) primaries were most active during active contraction and gastrocnemius (extensor) primaries fired more during passive stretch. In fact, there are muscles that normally shorten passively during locomotion in which brisk spindle discharge is maintained, presumably by selective fusimotor activity (Loeb and Duysens 1979). This suggests that no single rule of spindle function will apply to all muscles.

It is difficult to compare rates of length change or magnitude of extrafusal activity between muscles with different insertions and fiber compositions. Therefore, the biarticular and bifunctional muscles of the quadriceps group represent an interesting test case. The rectus femoris and sartorius (pars lateralis) both act as flexors of the hip and extensors of the knee. Both actively lengthen during stance as the hip is extended. Both rapidly shorten during flexion but active contraction occurs in rectus only at faster gaits (see Fig. 5). The actual magnitude of the length changes and velocities are among the largest and most monotonic in the body, representing 12–30% of rest length each step cycle.

The activity of two spindle afferents from these muscles is shown in Figs. 5 and 6 (unfortunately, methods for measuring conduction velocity *in situ* accurately enough to differentiate primary from secondary endings were not available at the time these records were obtained). The spindle from the rectus femoris (Fig. 5) was active only during the stance phase regardless of speed of gait (note swing phase EMG in rectus during fast trot). Visual comparison of this activity with extrafusal EMG and length and velocity of the parent muscle suggests that the unit responded to stretch velocity as well as total length but had little modulation temporally correlated with EMG. The simplest (but not sole) explanation would be passive stretch sensitivity, perhaps with  $\gamma$  dynamic fusimotor enhancement of velocity sensitivity but no clear  $\alpha$ - $\gamma$  static coactivation. An almost identical firing pattern was observed in a spindle ending from sartorius (pars lateralis) in the same animal on a different day. However, an entirely different response from a sartorius spindle recorded at the same time as the unit in Fig. 5 is shown in Fig. 6. This spindle generated

most of its firing during the very rapid flexion phase shortening, even for the fast trot where the shortening velocity exceeded 3 rest lengths per second. It was much less active during the active lengthening of the stance phase and was not apparently as sensitive to stretch velocity. This pattern could only be explained by a strong, rapid static fusimotor contraction specifically during the flexion phase extrafusal activity. This double burst pattern is very similar to that previously published for two pure ankle flexor spindles (Loeb and Duysens 1979). (Both spindles in Figs. 5 and 6 show a slight, brief tendency to pause at the peak stretch velocity, which is paradoxical and may reflect some tendency of intrafusal bag fibers, whose contractions result in high velocity sensitivity, to yield during these extreme stretches.)

It is unclear how far an argument for separate "flexorlike" and "extensorlike" patterns of spindle function can be extended. Its validity is likely to depend more on the task-specific presence of lengthening or shortening contractions rather than on the anatomists' identification of the muscle as an extensor or flexor. It is intriguing that muscles that have both kinds of activity may have spindles appropriate to each task, perhaps even with reflex pathways appropriate to the very different motor control problems each kind of contraction represents (see Eccles and Lundberg 1958). Other work from this laboratory has demonstrated that motoneurons to these muscles appear to participate in either the flexion or extension phase EMG bursts but not both (Hoffer et al. 1981). However, such a functional theory leaves us without testable predictions of the activity that might be expected from other preparations which have been studied, e.g., jaw muscles (Taylor and Cody 1974), fine hand movements (Hagbarth and Vallbo 1968), or respiratory muscles (Sears 1964). No simple, single servotheory seems likely to account for all the data, particularly if it ignores the specific motor control goals that are implicit in the performance of each task.

#### Acknowledgment

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