

Activity of Spindle Afferents From Cat Anterior Thigh Muscles. III. Effects of External Stimuli

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SUMMARY AND CONCLUSIONS

1. Chronically implanted electrodes were used to record the activity of identified single muscle spindle afferents in awake cats during responses to various types of manual and electrical stimulation.

2. During vigorous cyclical responses such as shaking and scratching, spindle afferents generally maintained at least some activity during both lengthening and shortening of the parent muscle, indicating that the programs for these movements include both extra- and intrafusal recruitment.

3. During noncyclical responses such as ipsilateral limb withdrawal and crossed-extension, spindle activity was modest and poorly correlated with extrafusal activity.

4. Weak cutaneous nerve shocks during walking elicited complex excitatory and inhibitory phase-dependent reflexes in the various muscles studied but caused relatively little change in spindle afferent activity, indicating a lack of correlation between alpha and gamma motoneuron activity.

5. A primary and a secondary afferent from sartorius muscle were recorded simultaneously during walking cycles that were perturbed by electrically induced twitches of the antagonist hamstring muscles; both demonstrated highly sensitive, short latency responses to the resulting skeletal motion, consistent with their previously suggested roles in detecting small brief mechanical perturbations.

6. The degree to which fusimotor responses were correlated with extrafusal responses to somatosensory perturbations was highly dependent on the specific nature of the stimulus and the response. Fusimotor reprogramming

of the spindle sensitivity appears to be a feature of cyclical movements that are presumably under proprioceptive control, whereas brief perturbations within the context of a particular motor program may be ignored by the fusimotor system.

INTRODUCTION

The response of a normally behaving organism to an unexpected sensory input usually includes a complex and widespread pattern of alpha motoneuron excitations and inhibitions, the details of which depend on the nature of both the stimulus and any ongoing activity at the time it occurred. The systematic electromyographic study of such reflexes has been a long-standing physiological tool for probing the organization of motor systems. In addition to alpha motoneurons, the mammalian efferent system to the skeletal muscles includes specialized gamma and beta motoneurons. These are distinguished by their terminations on intrafusal muscle fibers, where they give rise to effects on transducer properties of and afferent activity from the muscle spindle proprioceptors. These fusimotor neurons receive polysynaptic input from many of the same afferents known to generate alpha motoneuron responses (for review see Ref. 15). Furthermore, the spindle afferents that they influence exert strong, short latency effects on the alpha motoneurons themselves.

We and others have reported spindle activity in various muscles in animals during cyclical activities such as chewing, breathing, and walking, which data suggest that there may be significant differences in the degree and type of fusimotor action accompanying the extra-

fusal work of particular muscles (for review see Ref. 10). However, this does not speak to the important question of whether any particular pool of alpha, beta, and gamma motoneurons can be recruited in a different manner depending on the task at hand. A clear answer to this question would give some indication of the level of complexity of the command signals needed to perform a given task. It would also indicate whether the role of the muscle spindles can be dealt with adequately by control systems incorporating fixed relationships among motoneurons and their proprioceptive feedback signals.

In this study, we report on the activity of muscle spindle afferents during several different motor behaviors elicited as part of various well-known reflex responses to external stimuli. We chose reflex responses particularly because we hoped that they might be subject to forms of motor control that would be different from those operating in the cyclically programmed locomotor activities studied in the previous two papers of this series (11, 12). Individual spindle afferents were recorded from the fifth lumbar dorsal root ganglion (L₅ DRG) of unanesthetized cats implanted with floating microelectrodes and an array of transducers and electrodes in the ipsilateral hindlimb. The various recording and identification methods and the normal activity patterns of these afferents during unperturbed walking are described in those two papers. The activity of some of these units was also recorded during the following kinds of somatosensory perturbation: 1) tonically applied, light touch stimuli triggering complex cyclical responses such as shaking and scratching; 2) tonically applied, mildly noxious stimuli provoking ipsilateral limb withdrawal and crossed-extension responses; 3) intermittently applied cutaneous nerve shocks during ongoing walking giving rise to temporally sequenced and gated extrafusal reflexes; 4) intermittently applied muscle nerve shocks during ongoing walking giving rise to sudden perturbations of limb position.

MATERIALS AND METHODS

The fabrication, implantation, and characteristics of the implanted recording devices are described and/or cited in a companion paper (12). Briefly, 10 adult male cats were surgically implanted under

general anesthesia and aseptic conditions with an external connector assembly that permitted access to the various implanted devices listed in Table 1. After recovery from surgery, the animals were exercised daily by walking on a treadmill while connected to electronic recording equipment and being videotaped. Unit activity recorded in the L₅ DRG was identified by modality and origin by various manipulations under anesthesia and by the conduction velocity obtained from spike-triggered averaging of whole femoral nerve activity.

Stimuli

Scratching was evoked by lightly inserting a cotton-tipped applicator into the external ear canal ipsilateral to the DRG recording as the animal lay quietly on its contralateral side. This usually resulted in a directed and coordinated cyclical movement of the hindlimb that varied from mild waving in the direction of the stimulated ear to vigorous scratching of the pinna.

Shaking was evoked by wrapping a piece of adhesive tape around the ball of the ipsilateral hindfoot. The animal was then released to walk on the slowly moving treadmill belt, whereupon it usually performed a vigorous cyclical shaking of the foot during the somewhat prolonged swing phases of two to four subsequent step cycles.

Noxious stimuli consisted of firmly squeezing the toes of either the ipsi- or contralateral hindfoot with our fingers, with the animal either fully conscious

TABLE 1. *Implanted devices and identifying abbreviations for figure traces*

DRG	Floating microelectrode in the dorsal root ganglion
FP	Femoral nerve cuff, proximal tripolar electrode site
FD	Femoral nerve cuff, distal tripolar electrode site
VI	Vastus intermedius EMG (intramuscular multipolar)
VM	Vastus medialis EMG (intramuscular multipolar)
VL	Vastus lateralis EMG (intramuscular multipolar)
RF	Rectus femoris EMG (intramuscular multipolar)
SA-a	Sartorius pars anterior EMG (bipolar patch)
SA-m	Sartorius pars medialis EMG (bipolar patch)
L _v	Length of vasti muscles (stretch upwards)
L _v '	First derivative (velocity) of L _v
L _r	Length of RF and SA-a muscles (stretch upward)
L _r '	First derivative (velocity) of L _r
F _p	Force at patellar ligament strain gauge
T	Treadmill tachometer (5 cm/tick)
Stance	Ipsilateral foot contact with treadmill (from videotape)

and standing, or lightly anesthetized with pentobarbital and lying on its side. This produced a flexion withdrawal of the squeezed limb and a simultaneous extension of the opposite limb.

Electrical stimuli to the cutaneous and muscle nerves were delivered as balanced biphasic square waves (0.1 ms/phase) from a constant current, photoisolated stimulator. Cutaneous nerve stimuli were delivered to a bipolar nerve patch electrode (8) implanted on the saphenous nerve (which also contains fibers comprising the median articular nerve of the knee). Muscle nerve stimuli were delivered to a bipolar nerve cuff implanted on the branch of the sciatic nerve giving rise to the various nerves of the hamstring muscles. The hamstring muscles are antagonists of the anterior thigh muscles from which the spindle afferents were recorded. Both cutaneous and muscle nerve stimuli were delivered as single shocks every 2 s as the animal walked steadily on the treadmill at a rate somewhat faster than 1 step/s. This allowed the effects of stimuli presented at various phases in the step cycle to be gradually accumulated, with at least one unstimulated step cycle occurring between any two stimulus presentations. The stimuli were all in the range of 2 to 5 times the threshold for the largest diameter nerve fibers, which caused brief, modest excitatory and inhibitory reflexes in a widespread distribution of hindlimb muscles without resetting the step cycle timing (1, 6). The cutaneous stimuli provoked little or no visible or electromyographic reaction in the resting animal. The muscle nerve stimulation produced a clear twitch of the hamstring muscles that caused a variable amount of hip extension and knee flexion depending on the loading of the limb.

Gated response rasters

Each electrical stimulation condition was usually tested by the above-noted random presentation (with respect to the step cycle) of 50–150 single shocks as the animal walked at a constant speed on the treadmill. The complete run was recorded on analog FM and videotape, and the times of occurrence of several critical boundaries in every step cycle were identified by using a combination of length gauge records (usually vastus muscles) and videotape stills. These are indicated on the rasters (e.g., Fig. 5) as footfall (down arrow), footlift (up arrow), and the swing phase transition between knee flexion and extension (vertical line). The mean duration of the three phases between those inflections (E_{2-3} stance, F flexion, and E_1 extension, respectively, from the Phillipson step cycle, 16) was calculated; any stimulus occurring in a step cycle whose duration differed by more than 15% from the mean was rejected.

Each accepted stimulus presentation was ordered vertically in the raster by its adjusted time following the most recent footfall, based on the time to the closest preceding reference transition. The duration

of each phase was normalized to the average duration of that phase for all step cycles. Each line of the raster indicates activity occurring 30 ms before a stimulus (control level) and 100 ms after (responses). In many cases, the stimulus artifact can be seen at or shortly following the heavy dot indicating the exact time of the stimulus in each trace (e.g., Fig. 6).

The bar graph along the right edge of each raster shows a smoothed (five point triangular weighted) sum of the control activity (20 ms preceding the stimulus) in the various traces. The bar graph at the top of each raster shows the summed activity from all the traces synchronized to the stimulus, and thus shows the mean temporal characteristics of the response latencies. Trends in the timing and amplitude of particular responses related to the phasing of the step cycle can be read by looking for contours in the raster as a whole. It is important to remember that step cycle phase moves to the right as well as down the raster, so long latency activity actually comes from a significantly later point in the step cycle than the stimulus occurrence (e.g., a 130 ms sweep spans one sixth of a typical 780-ms step cycle duration).

Each spindle unit discharge is shown as a single, triangular waveform with a 4-ms duration centered at the point of occurrence of an acceptance pulse from the window discriminator. Electromyographic responses represent the amplitude of a full-wave rectified signal that was integrated into discrete 2-ms wide bins prior to digitization at 2-ms intervals (2). Scale factors of the raster traces and their summary bar graphs have been adjusted for display purposes; they are intended to present information about timing and relative amplitude only within any one raster.

RESULTS

Activity during cyclical responses

The strongest evidence for programmed fusimotor activity during extrafusal reflexes came during the cyclic responses of shake and scratch, particularly in the vasti muscles.

Figure 1 shows the activity of a spindle primary from the vastus lateralis muscle (identified by its sensitivity to passive limb motion and by the vibratory field indicated in the insert sketch) with a conduction velocity of 109 m/s (based on spike triggered average records from two femoral nerve tripolar recording sites shown at lower left). This spindle afferent was somewhat remarkable for having relatively little activity during the stance phase, when its parent muscle was extrafusally active. However, this afferent was quite sensitive to devia-

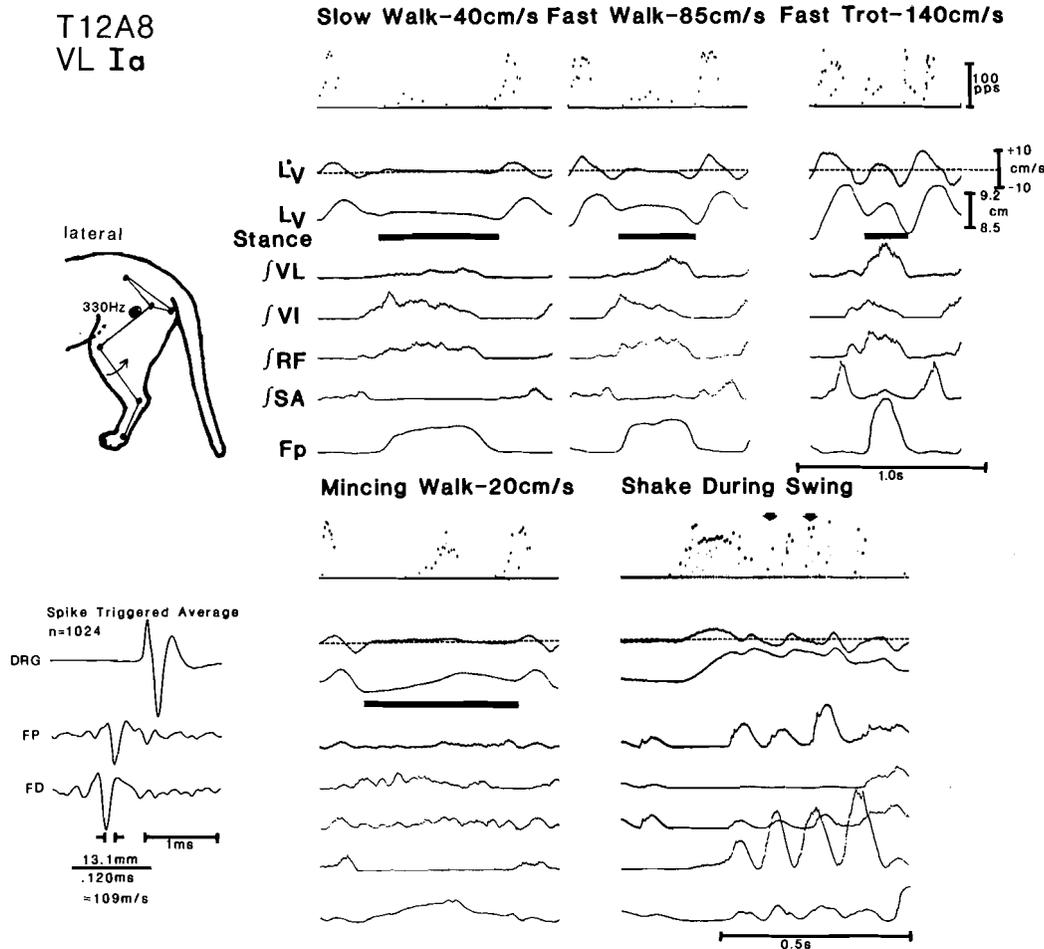


FIG. 1. Unit T12A8, spindle primary from vastus lateralis muscle (VL), sensitive to knee flexion and vibration up to 330 Hz applied to field indicated in insert sketch. Conduction velocity of 109 m/s determined from spike triggered averages (1,024 sweeps) of unit potentials recorded at tripolar electrodes in the proximal (FP) and distal (FD) halves of the femoral nerve cuff (*lower left*). Traces from top down in each panel: frequencygram of instantaneous firing rate of discriminated primary afferent; L_v , velocity of vastus muscle motion (differentiated length records, stretch is positive); L_v , length of vastus muscles (from implanted length gauge, calibrated from joint angles on videotape and geometrical model of musculoskeletal anatomy); stance, time of ipsilateral foot contact with treadmill surface shown as heavy black line; 4 traces of rectified and Paynter filtered EMG from VL (vastus lateralis), VI (vastus intermedius), RF (rectus femoris), and SA (sartorius); F_p , force from implanted strain gauge on patellar ligament. The *panel at lower right* (shake) was made at twice the trace speed; *arrows* indicate spindle afferent activity occurring during periods of active muscle shortening, with similar bursts in between during periods of passive muscle lengthening; see Fig. 2 for detail of raw data.

tions that increased the muscle length from its normal course, as indicated by the brisk response to an unusually large yielding of the knee joint (stretching the muscle) when the animal took very slow, short steps near the front edge of the treadmill (Mincing Walk bottom left). Note also that during walking this afferent was almost always silent during even slight muscle shortening. The traces at bottom right are from swing phase activity

with a four cycle shake response at ~ 10 Hz (note changed time base). This sequence is shown in greater detail in Fig. 2. The initial passive muscle stretch at the beginning of swing was accompanied by spindle afferent activity consistent with the mechanical stimulus alone. Of the five distinct bursts of EMG in the parent muscle VL, at least two occurred when the muscle was shortening at rates that, during locomotion, would have been asso-

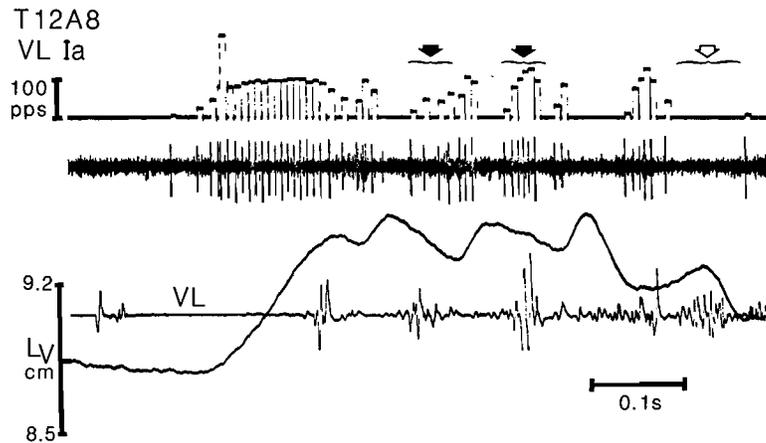


FIG. 2. Detail of the shaking sequence from Fig. 1, showing the instantaneous firing rate of unit T12A8, the filtered microelectrode recording used for spike discrimination, and the length and unprocessed EMG recording from the vastus lateralis muscle in which the spindle appeared to be located. *Solid arrows* indicate afferent activity during active muscle shortening; *open arrow* indicates absence of same for active movements after the end of the shaking sequence.

ciated with complete spindle silencing. However, brisk afferent discharge accompanied these bursts (solid arrows). In contrast, the VL EMG activity at the end of this trace corresponded to the normal preactivation and shortening of this antigravity muscle prior to footfall, and this was not accompanied by any unusual spindle activity (open arrow in Fig. 2). Note the absence of participation in the rapid shaking by the slow synergist VI (Fig. 1) in agreement with similar selective nonrecruitment in cat soleus muscle (slow ankle extensor) during paw shaking (17).

Figure 3 shows the activity of a spindle primary (120 m/s conduction velocity) located in the anterior part of the sartorius muscle (hip flexor and knee extensor; length and velocity given by L_R and L'_R , respectively). During normal locomotion, this unit had 50–150 pps activity during active stretch (stance phase) and 30–100 pps activity during active shortening (swing phase) of the parent muscle (see Fig. 4 in the first paper of this series).

At the onset of the stimulation to the ear, there was a buildup of the low spontaneous unit activity before any discernible length or EMG changes in the muscle. This was somewhat irregular and may have corresponded to small movements transmitted to the body by the stimulating probe in the ear or to the sort of fusimotor cycling in the absence of movement or muscle activity described prior to licking in a jaw muscle spindle (19). The vig-

orous participation of the muscle during the scratch was accompanied by sustained activity of the spindle that was clearly related to the velocity of stretch but persisted during shortening (when EMG was off or declining). Relative to the responses to passive motion (lower left), the activity during scratching suggests a possible combination of static and dynamic fusimotor effects.

Activity during noncyclical responses

Stimuli that resulted in tonic postural shifts such as crossed extension and withdrawal resulted in surprisingly little spindle afferent activity, even when the parent muscle was activated vigorously.

Figure 3 shows an initial acceleration of spindle activity during squeezing of the ipsilateral foot. During the withdrawal, the knee flexion was balanced by a hip flexion resulting in little net length change for the biarticular anterior sartorius muscle. The muscle was quite active extrafusally throughout the period, but spindle activity remained low until near maximal active flexion, when the muscle as a whole became somewhat shorter. As the foot escaped from the experimenter's grasp, there was a brief pause followed by a burst; both were probably related to small, fast oscillations of the limb seen on video analysis. Spindle activity then remained high when the muscle relaxed completely following this escape.

Crossed extension caused by squeezing the

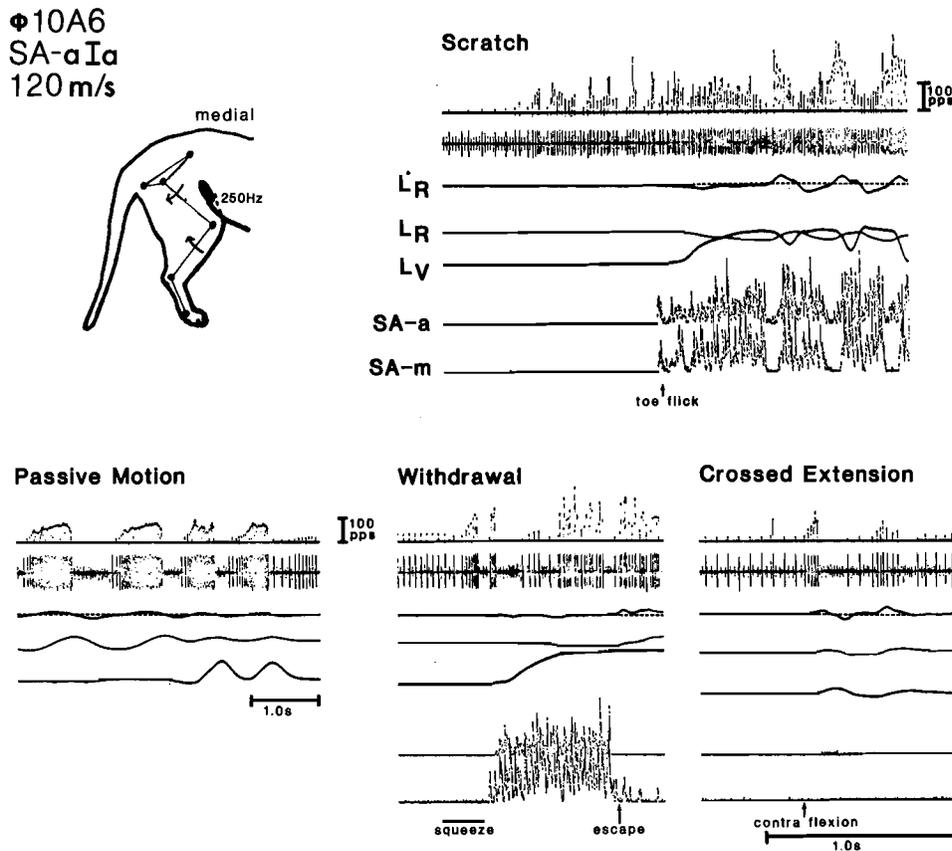


FIG. 3. Unit 010A6, spindle primary (CV = 120 m/s) from anterior sartorius muscle. The relative sensitivity to knee and hip motion of both the unit and the implanted length gauges can be estimated from Passive Motion sequence obtained under light pentobarbital anesthesia, which shows the afferent frequencygram and the outputs of the biarticular length gauge L_R and the knee only gauge L_V to 2 cycles of manually applied pure hip motion, followed by 2 cycles of manually applied pure knee motion. The scratch activity panel at top starts with the animal lying at rest, at which time we stimulated the ipsilateral ear canal. The first overt movement was a flick of the toes, followed rapidly by strong hip and knee flexion by using both the anterior (SA-a) and medial (SA-m) parts of sartorius, and a long series of phasic scratching movements, the first 3 of which are shown here. The *withdrawal panel at bottom* shows the response to squeeze of the ipsilateral foot and the point at which the flexion movement resulted in escape from the hand of the investigator. *Crossed extension panel* shows the response to a similar stimulus delivered to the contralateral foot, resulting in extension of the ipsilateral leg. The animal was lightly sedated with pentobarbital during all of these activity records.

contralateral foot generated little or no extra-fusal activity in either part of the sartorius muscle. The homonymous spindle activity (Fig. 3) generally followed the small length changes accompanying the activity of the extensor muscles. A similar pattern is seen in Fig. 4 for a spindle primary located in the knee extensor vastus lateralis. Vigorous extrafusal activity was uncorrelated with spindle activity, which generally declined as the muscle actively shortened. This was the same unit as shown in Fig. 1, which provided little evidence for

fusimotor coactivation during locomotor use of the muscle but maintained vigorous discharge during active muscle shortening in the shake reflex. The activity of this spindle during active shortening induced by lightly touching the back to provoke arching was similar to that seen during crossed extension, although the brief burst of spindle activity just at the first contact with the back (accompanied by a typical flexor reflex burst in SA and RF) does suggest some phasic response to the stimulus itself.

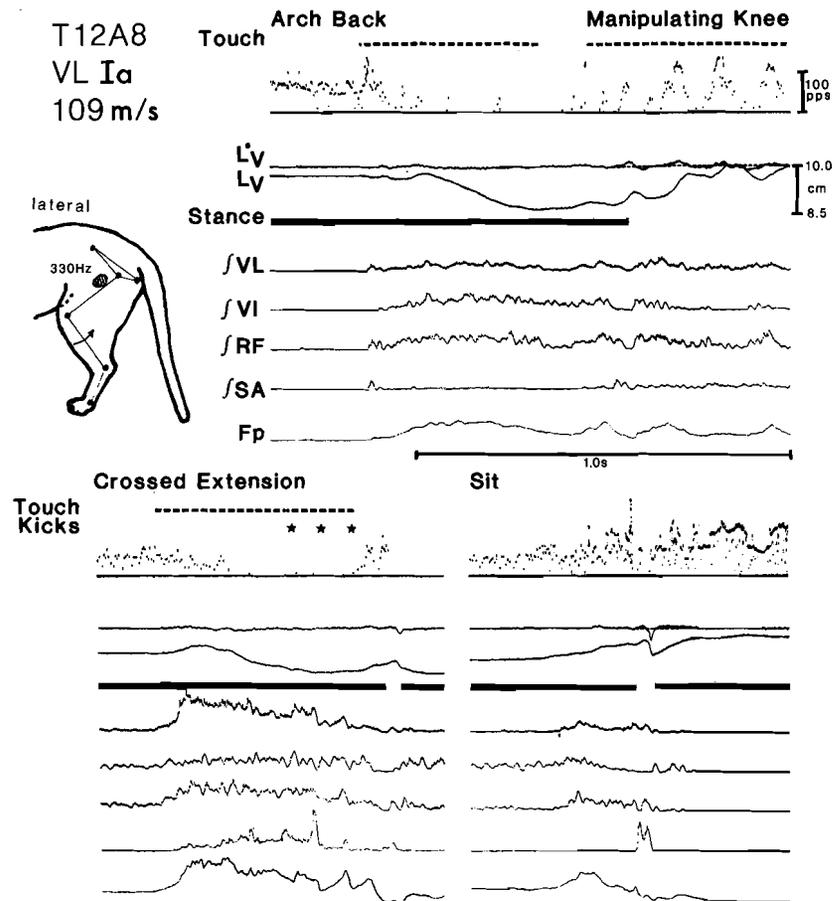


FIG. 4. Unit T12A8, spindle primary (CV = 109 m/s) from vastus lateralis muscle, during a series of manipulations in the fully conscious cat. *Dashed trace* indicates time of contact of the manual stimulation causing the response indicated: arch back sequence was provoked by light touch over the sacrum, causing the animal to stand up from a sitting position. This was followed immediately by a shift of the experimenter's hand to the leg to generate the series of passive (somewhat resisted) flexion movements indicated by the length gauge record. Crossed extension sequence shows the time of manually applied squeezing of the contralateral foot, resulting in withdrawal culminating in 3 quick contralateral kicks (*stars*) as the animal stood on the extended ipsilateral hindlimb. Sit sequence was a slow, voluntary postural shift from standing to sitting, with a brief repositioning of the ipsilateral foot at the break in the stance trace.

Activity during locomotor reflexes

The cutaneous nerve stimuli delivered during the step cycle caused complex but orderly patterns of excitatory and inhibitory EMG changes in the various muscles depending on the normal use of the muscle and the phase of the step cycle in which the stimulus occurred. These have been described in detail elsewhere for anterior thigh and other muscles (1, 6, 14). For the knee extensor muscles in the vastus group, the extrafusal reflexes consisted mainly of a short latency, brief inhibition of ongoing muscle activity during the stance

phase, particularly in the red vastus intermedius. Spindle afferents from these muscles had little or no change in their activity in responses to saphenous nerve stimulation. The biarticular muscles with hip flexion action all responded with excitatory reflexes, most prominently during the swing phase active shortening of these muscles, when the normally sustained spindle activity suggested static fusimotor coactivation. However, we found little consistent acceleration of the spindles at latencies that would be consistent with the mechanical latency of the fast twitch intrafusal chain fibers (30–100 ms; Ref. 3).

Figure 5 shows the response cycle rasters for two spindle primaries, one from the anterior part of sartorius (same unit as Fig. 3) and one from medial sartorius, along with the reflex responses of the parent muscle EMG showing excitation and of the vastus intermedius showing inhibition. In both cases, rasters for the parent muscles show the typical double burst excitatory pattern (arrows) for saphenous nerve stimuli occurring during swing phase, but there was no discernible change in ongoing spindle activity, which continued with its normal pattern of modulation.

Figure 6 shows the only spindle afferent with a clear response during these electrically induced flexor reflexes. The unit was a spindle

primary (119 m/s conduction velocity) from anterior sartorius; it was one of the most vigorously active units recorded, having spike rates of up to 300 pps during both swing and stance phases (see Fig. 4, Ref. 12 and Fig. 4, Ref. 11 for locomotor traces). The EMG response to the stimulus during walking consisted of a large, short latency excitation (~ 10 ms latency) and a small and less consistent excitation about ~ 30 ms latency (Fig. 6 top). The spindle activity showed a large and abrupt peak at ~ 20 ms latency; response tended to be largest when the early extrafusal response was largest. The normal swing phase activity of this spindle afferent could be blocked almost completely by low concentrations of lidocaine infused around the femoral nerve via a per-

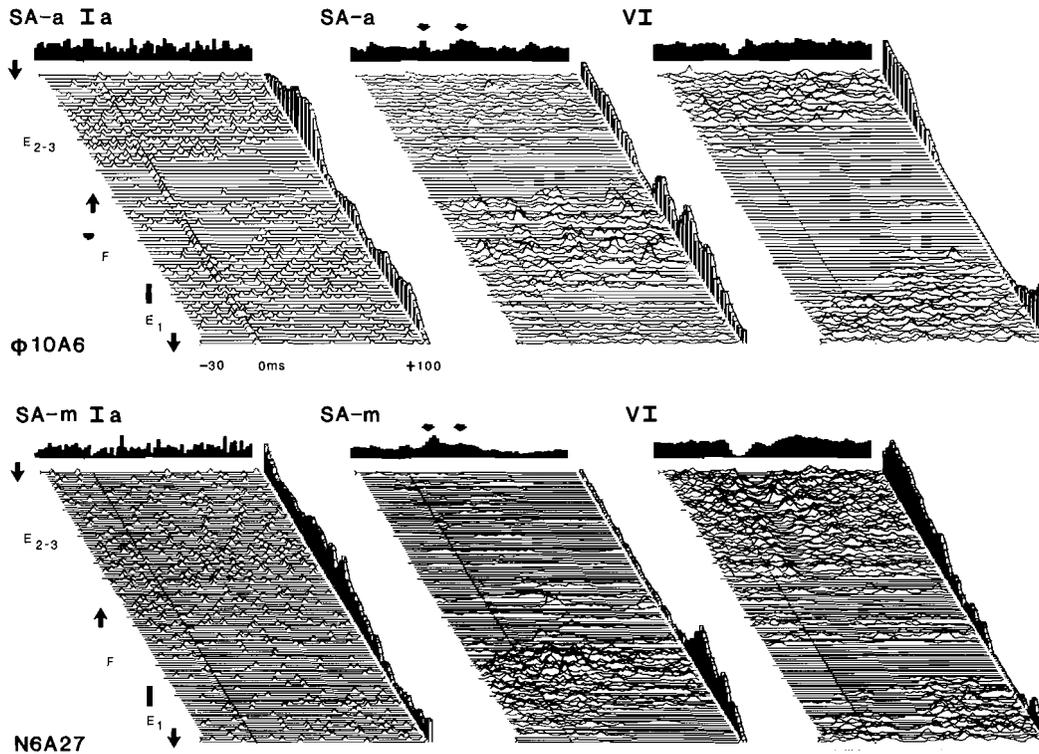


FIG. 5. Rasters of pre- and poststimulus activity ordered by phase of saphenous nerve stimulus presentation during slow walking. Each row of rasters shows activity during the same sequence of stimulus presentation. The first raster in a row shows the activity of a spindle afferent, the second the EMG activity of the parent muscle, and the third the EMG activity of the slow knee extensor, vastus intermedius. Each line of a raster shows activity 30 ms before and 100 ms after a single stimulus presentation, occurring at 0 ms (small dot on each line). Bar graph at the top is the summed activity of all traces. Bar graph at the right is the summed and smoothed activity of the prestimulus control activity of each trace. See text for explanation of the ordering of the traces based on the phase of stimulus occurrence as indicated in the symbols at the left of each row of rasters. Note the excitatory EMG reflexes (arrows) during the swing phase of both parent muscles (second raster each row) and the absence of any activity change in the spindle afferents (first raster each row).

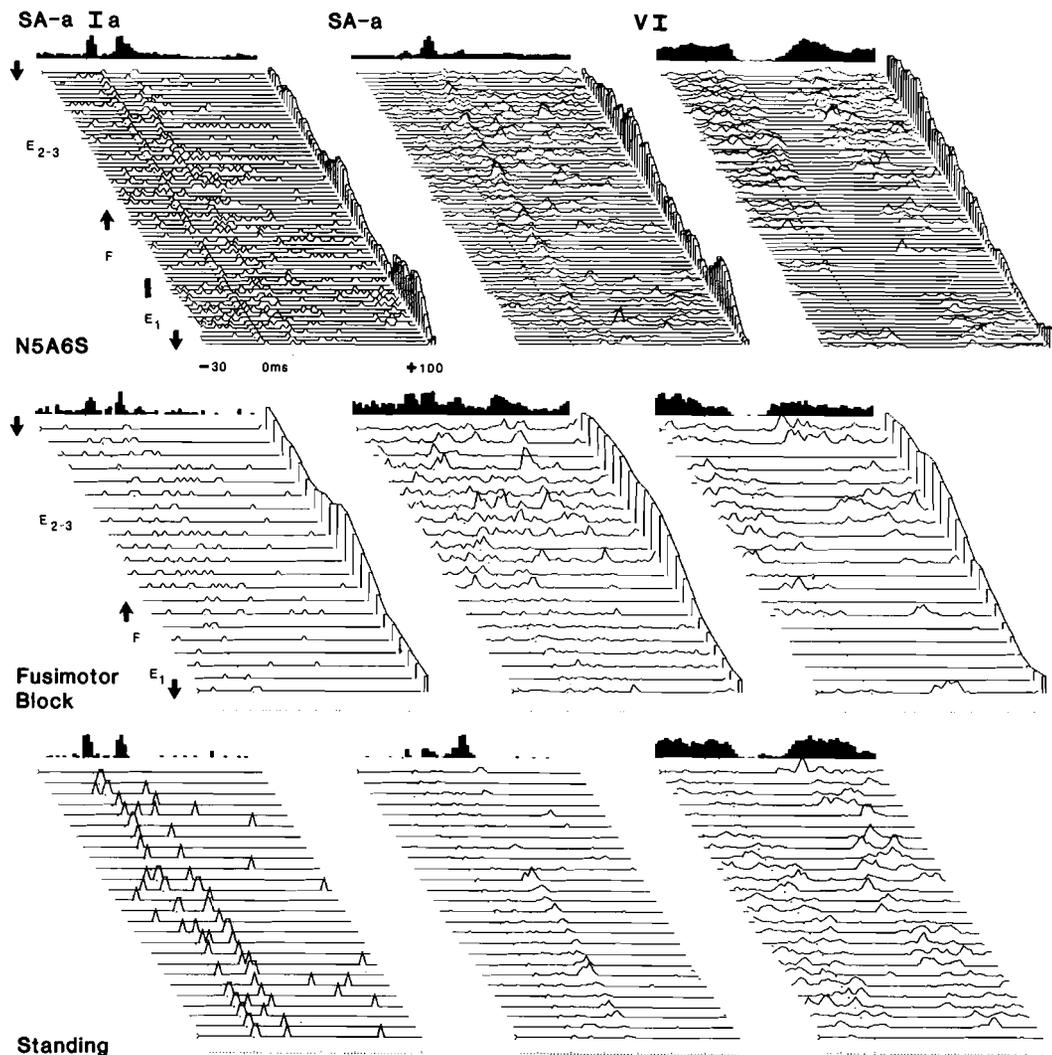


FIG. 6. Locomotor reflex response rasters for the only spindle afferent showing a consistent response to saphenous nerve stimulation. *Top row* of rasters shows unit activity, parent muscle EMG activity, and vastus intermedius activity in response to 68 presentations of the saphenous nerve stimulus during slow walking. The *middle row* shows responses to the same stimulus during lidocaine blockade of small-diameter femoral nerve fibers during slow walk. The *bottom row* shows the same set of signal sources for 26 presentations of the same stimulus during quiet standing (ordered chronologically). Note the consistent response of 1–3 spikes in the afferent at about 20 ms poststimulus in most traces, together with the double-peaked EMG response in the anterior sartorius and a strong inhibition of any ongoing activity in VI. Unit responses at 0 ms come from stimulus artifact.

cutaneous catheter (Fig. 4, Ref. 11). When this was done (Fig. 6 middle), the reflex activity of the spindle during the swing phase also ceased, but the stance phase responses remained. (However, the saphenous afferents pass through the femoral nerve, and even at these low stimulus strengths, some fibers contributing to the normal reflex may have been

blocked by the lidocaine.) The same stimulus was presented while the animal was standing quietly (before lidocaine), with little or no background activity of the afferent or its parent muscle (Fig. 6 bottom). Under those conditions, both of the excitatory EMG peaks and the accompanying spindle activity occurred at latencies similar to those during normal walk-

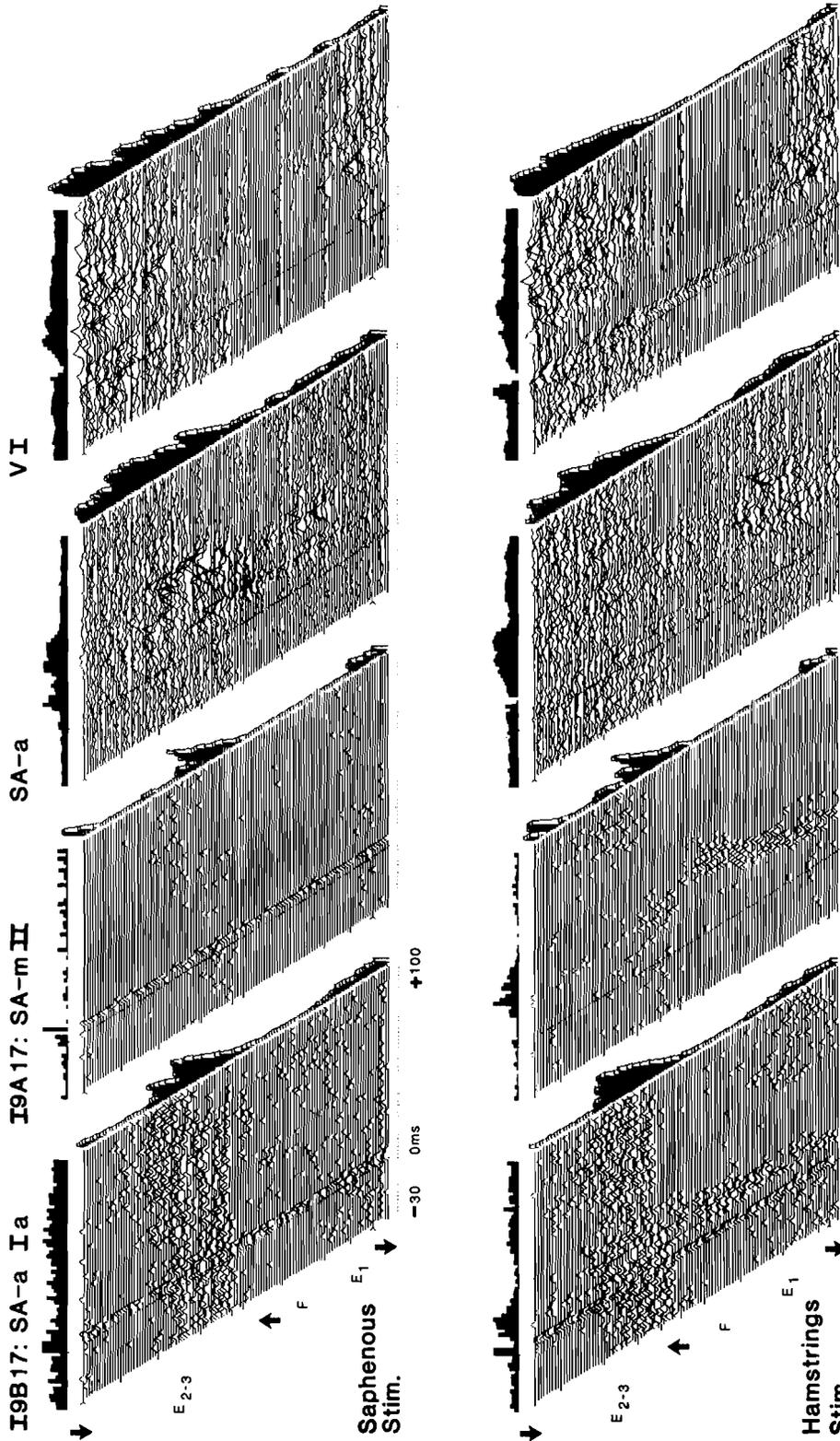


FIG. 7. Locomotor reflex-response rasters for 2 simultaneously recorded spindle afferents plus EMG from anterior sartorius and vastus intermedius muscles. *Top row* shows response to 117 stimulations of the saphenous nerve during walking. *Bottom row* shows response to 108 stimulations of the motor nerve to the hamstring muscles. Saphenous nerve stimuli resulted in the usual pattern of excitatory and inhibitory reflexes in sartorius and vastus muscles, respectively, but no response in either spindle afferent. Hamstring muscle twitches resulted in both short latency afferent activity and typical flexor reflex patterns in the EMG responses.

ing, although the relative amplitude of the two EMG bursts was reversed (i.e., the longer latency response was much larger than the early one). It is possible that the spindle responses might reflect early mechanical activation by a fortuitously located extrafusal reflex twitch (note loss of swing phase EMG in SA-a during lidocaine). However, the lack of a subsequent spindle pause and the consistent nature of the response during kinematically diverse phases of the step cycle all seem more consistent with a response to a single twitch of an intrafusal chain fiber.

Figure 7 shows the response of two simultaneously recorded spindle afferents to stimulation of the saphenous nerve (top) and hamstrings nerve (bottom). The first raster in each row comes from unit I9B17, a spindle primary (CV = 109 m/s) in anterior sartorius; the second raster is from I9A17, a spindle secondary (CV = 67 m/s) in medial sartorius. Both units were normally active in both stance and swing; neither had any cutaneous reflex response during any phase despite the usual flexor reflex EMG patterns in the sartorius muscle.

The responses to direct stimulation of the hamstring muscles at various parts of the step cycle were consistent with the effects of a twitch of the antagonist muscles. The spindle primary generated a vigorous response with a latency of only 10 ms and a duration consistent with the presumed rising phase of the muscle twitch. The response was least at the beginning of stance phase, when the loading of the body weight and low mechanical advantage for the stretched hamstring muscles would minimize the limb motion that could occur from such a twitch. However, the spindle response was very brisk even when the afferent was normally inactive, as during the early part of the swing phase when the sartorius muscle normally shortens rapidly.

The spindle secondary was also mechanically responsive to the hamstrings' twitch during most of the step cycle, but with a longer and more variable latency and frequently longer duration of its responses. The minimum latency was ~18 ms, and the latency during the early swing phase was as long as 30 ms, with response activity lasting until 50 ms post-stimulus. This was consistent with the tendency of this secondary ending (during normal

walking and manipulations) to be more dependent on the magnitude rather than the rate of muscle stretch, as well as the tendency for the hamstrings to cause a knee flexion that would counteract and perhaps delay the stretching of the medial sartorius by the hip extension. Interestingly, the muscle nerve stimulation, which most likely activated group I and II proprioceptive afferents as well as motoneurons, gave rise to short latency excitatory and inhibitory reflexes in the anterior thigh muscles that were quite similar to those evoked by the segmental cutaneous stimulation of the saphenous nerve. We have noted previously a similarity in the locomotor reflexes induced by cutaneous and muscle nerve stimulation around the ankle (6).

DISCUSSION

Evidence from recordings of human muscle spindle afferents during voluntary muscle activation has indicated that the patterns of recruitment of alpha and gamma motoneurons may not be subject to voluntary differential control. At least for the class of voluntary, slow, and restricted movements studied, the activity of the muscle spindles was consistent with proportional coactivation or, perhaps, size-ordered activation of all of the motoneurons (alpha, beta, and gamma) belonging to a motor nucleus (for review see Ref. 20). The inability to change the sequence of motoneuron recruitment under voluntary control has been taken as further support for the hypothesis of alpha-gamma coactivation as a general principle of motor control, perhaps embodied in the connectivity from the central pattern generator for the movement itself.

We have used various types of somatosensory stimulation to elicit different motor behaviors involving the same group of muscles and their spindle afferents. These data suggest that the relationship between extrafusal recruitment and fusimotor influences on a given spindle afferent is not invariant. Extrafusal activity during cyclical motor programs (shake and scratch, Figs. 1-3) was accompanied by high levels of spindle activity strongly suggestive of significant levels of fusimotor influence, particularly of the static type. Similar levels of extrafusal recruitment during tonic postural responses (Figs. 3 and 4) and during phasic

reflex responses to single cutaneous nerve shocks during walking (Figs. 5-7) were accompanied by more modest spindle activity, suggesting little or no fusimotor recruitment beyond the background levels that were present at the time of the stimulus.

The distinction between the fusimotor activity associated with repetitive tasks and that during one-time phasic and tonic responses cited above is an interesting one, although it should be noted that it is based on a small sample of units, few of which were studied with a complete battery of stimuli. We have suggested elsewhere (10, 13) that the optimized control of spindle sensitivity might require a carefully programmed recruitment of the various intrafusal muscle fibers together with specific deconvolution networks to allow the central nervous system to extract useful information about limb motion from the combined effects of such fusimotor influences and external mechanical motion on the spindle afferents. It seems plausible that only a limited number of such preprogrammed systems might exist in the various command centers for frequently occurring types of motor behavior. Responses to perturbing stimuli such as employed here might then be divisible into preprogrammed responses (e.g., shaking and scratching) and one-time events within the context of the ongoing behavior (e.g., locomotor reflexes and postural shifts). For these latter responses, it would be important to be able to generate the appropriate extrafusal response without upsetting the fusimotor tone of the spindles. If the fusimotor program for the spindle has already matched the transducer sensitivity to the range of mechanical inputs expected, then there is no need to change this program for one-time, transient events. Similarly, there would be no need to change the fusimotor program to accommodate a desired change in the motor response to a mechanical perturbation. The Jendrassik maneuver may be another example of a tendency of the system to avoid unnecessary fusimotor reprogramming by modulating central transmission instead (5). However, the command centers for different *types* of movements do appear to have the capability of tailoring the fusimotor parts of their motor programs for the expected movements of the muscles.

In the previous two papers, we developed

the notion of optimal control of spindle sensitivity as consisting of two goals: 1) Spindle afferent activity should tend to occur within a relatively narrow band of spike rates (perhaps 50-200 pps for primaries, somewhat lower for secondaries) to avoid saturation-like phenomena when the spike rate becomes too low to permit rapid assessment of changes in rate or too high for spike production to accurately follow generator potentials (13). 2) Spindle afferent activity should be modulated over most of this band of spike rates for the range of kinematic conditions that tend to occur during any given task. This maximizes the resolution of the proprioceptive information being sent to the CNS.

These two goals obviously involve a trade-off between processes that simply bias the spindle into the desired range but reduce sensitivity (a general effect of static fusimotor activity) and processes that increase sensitivity to small perturbations at the risk of saturation (a general effect of dynamic fusimotor activity). The optimal compromise in terms of information transmission can only be arrived at by consideration of the range of movements anticipated. In such an optimized state, unexpected perturbations should drive the afferent signal out of the target range, but otherwise it will tend mostly to stay within it.

If a perturbation arises that is outside of the events anticipated (e.g., as a result of external stimuli or motor responses thereto), there are three options: 1) If the perturbation is small enough that it lies within the programmed transducer sensitivity, it can be ignored safely by the control apparatus for transducer sensitivity because it will be adequately tracked. 2) If the perturbation is large but transient, so the motor response is essentially ballistic rather than guided by feedback, it can be ignored safely. This is because the temporary saturation of the proprioceptive feedback signal will not compromise the response (which will be over before any such feedback could influence it). In fact, it is in the interest of the controller to avoid any changes in transducer performance that might cause confusion in interpreting the afferent signals after the system returns to its normal state. 3) If the perturbation is a large and temporally extended response that must be guided by feedback control, then the transducers must be reprogrammed for

appropriate operation under the conditions anticipated during this extended response.

We can sort the various spindle responses presented here into these three categories: 1) Postural shifts such as crossed extension and arching the back (Figs. 3 and 4), small volitional changes in an ongoing activity (e.g., mincing walk in Fig. 1), and internal mechanical perturbations of ongoing activity (e.g., hamstring muscle twitch, Fig. 7) seem to be handled with little or no change in the fusimotor program, whether or not they are accompanied by extrafusal activity changes. Note that this may give rise to sustained silencing of spindle afferents in active but shortening muscles (Figs. 3 and 4).

2) Stimuli that may lead to fast, ballistic escape behavior (e.g., flexor reflex, Figs. 5-7) also do not change the fusimotor program. We deliberately chose stimuli that were mild enough to elicit only small, short latency EMG reflexes so that large numbers of repetitions could be accumulated; thus we do not actually have examples of ballistic behavior that fell outside of the transduction range of the spindles. However, given the fact that the intrafusal muscle fibers are fairly slow and given examples (see next point) of fusimotor reprogramming that appear to anticipate extrafusal behavior, the failure to see any short latency change in most spindles seems significant. It is useful at least to preserve the distinction between ballistic activities and small or brief perturbations of ongoing motor programs (point 1) in view of their different implications for motor control.

3) Stimuli that lead to new behavioral states (shaking, scratching, or simply getting up to start walking) call for reprogramming of the fusimotor system to assure a steady flow of sensory information. In this regard, it is particularly striking to contrast the back arching response of a VL spindle primary (Fig. 4) with a similar movement made for different purposes—getting up to start walking (see VM spindle primary in Fig. 3 of first paper in this series). Standing up to begin walking (a new behavioral state) was accompanied by a large increase in afferent activity from an irregular 10 pps to ~120 pps; standing up to arch back (a postural shift) was accompanied by a drop from 100 pps to 0. Both of these movements involved virtually identical active shortening of the parent muscles. This reprogramming

extends to and is sufficient to cope with rapid cyclical movements such as paw-shaking (see Fig. 2), for which detailed kinematic analysis has suggested that proprioceptive information about knee motion is necessary to produce effective muscle activation patterns (9, 18).

There is one premise implicit in all of the above: the fusimotor program should be dictated by the anticipated movement, not by the recruitment of the alpha-motoneurons. If it happens that the muscle will actively shorten to cause the movement, then there may be a correlation between the observed EMG and the activation of intrafusal chain fibers needed to maintain spindle afferent discharge during the ensuing movement. If it happens that the muscle will yield while actively generating force during the movement, then there may be a correlation between its EMG and dynamic fusimotor activity needed to enhance the spindle afferent response to stretching. However, these coincidences hardly constitute a fundamental principle of motor control, as the term "alpha-gamma coactivation" has come to imply in some texts (7).

From this series of studies on spindle behavior and control in the intact animal, three general conclusions can be drawn: 1) Spindle afferents tend to generate activity over a rather narrow range of spike rates for kinematic stimuli spanning the large range of physiological lengths and shortening and lengthening velocities. 2) This tendency is the result of multifarious, complexly modulated fusimotor drive operating almost continuously. 3) This tendency is suggestive of a general strategy of the system, namely the optimization of the sensory information flow from the muscle spindles regardless of the work of the parent muscles.

Such a sensor-oriented strategy places the burden of processing the afferent information within each of the many perceptual and motor centers that make use of such information for purposes as diverse as kinesthesia, motor learning, reflexive regulations, and many others.

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