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Muscle Afferent Contribution to Control of Paw Shakes in Normal Cats

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SUMMARY AND CONCLUSIONS

1. The discharge of various hindlimb muscle afferents was recorded during paw shakes in normal cats with the use of floating dorsal root electrodes.

2. Muscle spindle group Ia-afferents and tendon organ group Ib-afferents fired during muscle lengthening, reaching very high peak discharge rates and then silencing at or shortly after the onset of shortening. The timing of Ia firing was consistent with the predictions of a linear model as well as the responses of Ia endings subjected to identical length variations in separate anesthetized cats.

3. In the latter "reconstruction" experiments, waxing and waning dynamic fusimotor action straddling whole paw-shake sequences gave the most consistent matches with the data from the normal cats. The reproducibility of the inferred fusimotor action justifies the inclusion of paw shakes as a class of movement in which fusimotor set is high.

4. The peak ensemble Ia activity from single hindlimb muscles was estimated to be ~20 kiloimpulses/s (Kips). Ankle extensor and hamstrings length variations were nearly in phase in the first cycles of a paw-shake sequence. From published data on spindle populations in these muscles, this indicated that peak Ia input to the spinal cord exceeded 0.2 megaimpulses/s (Mips).

5. The phase relationship between origin-to-insertion muscle length and Ia firing during paw shakes was little affected by doubling or tripling the moment of inertia of the foot. We argue that this refutes the notion that in paw shakes phase reversals occur between muscle fibers and tendons in the muscles studied.

6. Inertial loading of the foot led to small but significant reductions in mean paw-shake frequency. This is consistent with an afferent contribution to the generation of these movements.

7. We conclude that in paw shakes in normal cats, the CNS "chooses" to sensitize Ia-afferents to muscle length variations by increasing dynamic fusimotor action. The resulting ensemble Ia input is very large and is likely to play a significant role in reflexly shaping the α-motoneuronal activity responsible for the paw shakes.

INTRODUCTION

Paw shaking in cats involves extraordinarily fast movements; up to 27 *g* peak linear acceleration has been measured at the paw (25). Of late there has been a growing research interest in paw-shake responses, both for the kinesiological data they provide (6) and the insight they give into CNS control of rapid and rhythmical movements (35, 36, 50, 54, 55). The movements themselves are readily elicited by applying sticking tape, water, or small weights to the foot (50) and may even be elicited after deafferentation of the lower part of the limb, by a mildly noxious stimulus applied to the skin of the upper thigh (32, 56).

The data to be presented in this paper bear upon three separate issues of current interest in motor control. Under certain conditions, tendon stretch has been shown significantly to affect the phase and amplitude of displacements of muscle fibers relative to displacements measured between muscle origin and insertion (1, 14, 15, 21). If muscle fibers and the muscle spindles in parallel with them "see" displacements different from those occurring between the origin and insertion of the muscle, this has an important bearing on the nature of the variable(s) sensed by the spindle endings and controlled by the nervous system (57).

In a recent report, bursts of firing of a muscle spindle primary (Ia) afferent during rapid muscle shortening in paw shakes were interpreted as indicating a deeply modulated phasic time course of static fusimotor action (36). Ia firing seemed poorly related to monitored length, sometimes peaking during shortening and sometimes during lengthening. Previous anecdotal data on Ia activity during paw shakes in conscious cats had shown little or no firing during phases of muscle shortening, but high discharge rates during presumed lengthening (50). Other workers who have recorded Ia firing during rhythmical movements of somewhat lower speeds have generally observed rapid Ia firing in lengthening and comparatively little firing in shortening (18, 34, 53, 59). This is also true of human neurography recordings, though here the maximal muscle velocities were lower still (e.g., Ref. 22). The issue is important in relation to current theories of fusimotor control in voluntary movement (3, 19, 36, 38, 45, 60).

A reported lack of effect of doubling paw inertia on paw-shake frequency in chronic spinal cats (9, 23) was adduced as evidence of central pattern generation, at least for the muscles acting about the ankle (56). In contrast, the disruptive effects of such loading on the more proximal musculature suggested a differential control of proximal and distal muscles in these movements (56). Paw-shake responses in spinal cats in which one hindlimb was extensively deafferented lent support to the hypothesis that patterns of ankle muscle activity were immutable (56). However, though the *patterns* were immutable, in a later report it was made clear that *cycle times* increased substantially after the extensive deafferentation (33). These results were largely obtained in chronic spinalized cats, in which supraspinal modulation of proprioceptive reflexes was absent.

To address these issues, we recorded the firing of hindlimb muscle afferents during paw shakes in normal cats implanted with dorsal root electrodes (44). Ia-afferents fired during muscle lengthening but fell silent at or shortly after the onset of shortening. The peak ensemble Ia input

to the spinal cord from single muscles (e.g., gastrocnemius) during a paw shake was estimated to be ~20 kiloimpulses/s (Kips), and that from all the muscles of the hindlimb in excess of 0.2 megaimpulses/s (Mips). There was evidence for waxing and waning dynamic fusimotor action encompassing whole paw-shake sequences, though a deeply modulated phasic pattern of static fusimotor action could not be ruled out entirely.

Lead cuffs which doubled and tripled the moment of inertia of the foot had little effect on the phase advance of spindle firing on origin-to-insertion muscle length. This did not support a prominent effect of tendon compliance in the muscles studied. However, the mean frequency of the paw shakes was reduced significantly by inertial loading. This supports the notion of a pattern generator in which both central and peripheral elements are inextricably linked (12, 61). A preliminary report of this work has been published (12).

METHODS

The chronic data in this report were obtained from 13 freely moving adult cats and the acute "reconstruction" experiments were performed in seven pentobarbital sodium-anesthetized adult cats. All of the surgical and recording techniques used have been described in detail previously (27, 44), so only a summary is presented here.

Implantation

In one surgical procedure, performed with pentobarbital sodium anesthesia (40 mg/kg ip, then iv maintenance doses), and with antiseptic precautions, a prefabricated loom of four 17-μm diam enameled Nickel-chrome micro-wires was implanted so that the deinsulated, beveled tips of the wires were positioned in the L_7 dorsal root ganglion, the connecting cable (4-core insulated, shielded AS 632-4 ss, Cooner Sales, Chatsworth, California) leading subcutaneously to a dental acrylic headpiece. Pairs of electromyogram (EMG) electrodes (Cooner AS632 stainless steel, Teflon-insulated wire) were implanted into the lateral gastrocnemius muscle (5–10 mm apart, centered ~40% of the way from knee to ankle) and posterior biceps femoris muscles (~10 mm apart, centered about halfway from ischium to upper third of tibia). The wires were also led subcutaneously to the headpiece. Nylon monofilaments (Ethylene 4/0) were embedded into the bony points of origin and insertion of these muscles at one end, the other end emerging percutaneously along the line of the muscle, to provide attachment points for external saline-in-rubber length gauges. A Silicone rubber cannula was inserted into the right external jugular vein (Vygon Nutricath 'S', Ecouen, France) and led to a port embedded in the headpiece, allowing antibiotics or short-acting anesthetic to be administered in the days and weeks following recovery. Cats recovered from the procedures over a 12- to 24-h period. After 1–3 days, when the effects of the anesthetic had fully worn off, they bore the small implants with no sign of discomfort or motor deficit.

Chronic recordings

Single-fiber neuronal recordings depended upon the tips of the implanted dorsal root wires slowly migrating into favorable positions near cell bodies or axons in the dorsal root ganglion. Three or four times a day following recovery, the neurogram electrodes were checked for single-unit activity. This was done by attaching a small three-channel radio telemetry device to a Luer socket embedded in the headpiece and making connections with each neurogram terminal in turn. The neuronal activity was monitored with the use of a nearby FM receiver, and the length and EMG were monitored with a second similar receiver. For the purposes of the present study, only units in muscle groups whose length and representative EMG were available were recorded during paw shaking. When such a unit appeared, a saline length gauge was attached to the appropriate fixation threads, the fine connecting wires (Cooner AS632) were led to the telemeter and taped to the skin of the leg and back with two or three small patches of sticking plaster. The telemeter's EMG input was mated up with the appropriate socket in the headpiece. The cat was then allowed to move freely about the floor of a room ~4 × 3 m. From time to time, small pieces of sticking plaster were attached to the paw to elicit paw-shake responses. In six cats, prefabricated lead cuffs with Velcro retaining straps were wrapped around the distal metatarsals. Initially, the presence of the weight alone elicited paw shaking, but the cats quickly adapted and additional sticking plaster stimuli were then needed to evoke further paw shaking. The animals tolerated these procedures well, and after a few initial seconds of apparent puzzlement, behaved as though the cuffs were of mild nuisance value only. Hyperflexion during stepping usually persisted throughout the recording sessions.

Much importance was attached to accurate identification of the afferent type and the location of its ending. When enough voluntary movement data had been obtained from a given afferent, the cat was fully anesthetized with thiopental sodium administered to effect via the indwelling jugular catheter. The receptor was located by careful palpation and joint manipulation. When necessary, supplementary doses of anesthetic were given to abolish muscle tone. The responses of the afferent to length changes of various waveforms applied manually were then recorded. When enough such data had been amassed, a dose of suxamethonium (200 μg/kg iv) was administered, and in the subsequent 3–4 min, a similar set of muscle length variations was applied. Muscle spindle primary and secondary afferents and tendon organ afferents are differently affected by suxamethonium, so this procedure is useful in differentiating between them (45). Typically the identification tests took between 15 and 45 min.

Telemetered data were decoded and recorded onto standard audio cassette tapes with a TEAC R61 instrumentation recorder. All trials were videotaped (Sony C7 Videorecorder). Subsequent analysis was performed by replaying the data and screening it first with a storage oscilloscope (Tektronix 5111). Relevant segments were then digitized with a Cambridge Electronic Design 1401 interface operating via BBC, IBM PC, or Olivetti M28 host microcomputers. The data acquisition software was developed by G. Smith of Cambridge Electronic Design and S. Vincent.

"Reconstruction" experiments

The method has been described in detail elsewhere (26), so only a summary is given here. Selected segments of chronic recording were digitized and stored on magnetic diskettes. These data were then used in separate acute experiments in which a reconstruction of the original muscle length changes, afferent responses, and fusimotor action was attempted. The length variations were replicated in soleus muscles of anesthetized cats (pentobarbital sodium, 40 mg/kg ip, with intravenous maintenance doses), with an electromagnetic length servo-driven from the analog outputs of a hybrid signal generator, which in turn was controlled by a LSI 11/73 laboratory computer. The responses of a population of muscle spindle afferents were recorded from teased dorsal root filaments with the use of bipolar electrodes in a paraffin pool bathing the lumbar spinal cord. The spindle responses to the paw-shake length variations were compared on-line to those recorded originally in the free-to-move animal. In some experi-

ments, fusimotor axons with action on the test spindles were functionally isolated and stimulated during the movement replications. An iterative procedure allowed on-line adjustment of the time course of rate modulated fusimotor stimulation to optimize the match between the acute and the chronic spindle afferent firing patterns (26).

RESULTS

Unloaded paw shakes: triceps surae Ia-afferents

Recordings were obtained from a total of 18 fully identified hindlimb muscle afferents during paw shakes in 12 cats. The receptor types and the parent muscles were as follows: 12 spindle primaries (Ia): 4 gastrocnemius, 2 soleus, 2 plantaris, 1 tibialis anterior, 1 peroneus longus, 1 posterior biceps femoris, and 1 anterior biceps femoris; 1 spindle secondary (II): plantaris; 5 tendon organ (Ib): 2 triceps surae, 1 plantaris, and 2 posterior biceps or semitendinosus (in the hamstrings muscles, specific localization of tendon organ endings to particular members of the synergistic group was not considered reliable).

All Ia-afferents fired during muscle lengthening but fell silent at or shortly after the onset of shortening. Figure 1 shows the discharge behavior of two gastrocnemius Ia-afferents during paw shakes. Both afferents fired mainly during the phase of each movement cycle in which the receptor-bearing muscle was lengthening. The records also show traces obtained by passing the length signals through an electronic filter, of which the transfer function mimicked that of deefferented Ia-afferents in their linear range (43). The filter output was half-wave rectified to show only the positive-going part of the signal, and the amplitude was adjusted to be comparable with that of the peak instantaneous firing rate of the segment. The model outputs were closely in phase with spindle firing rate, so from this initial data there was nothing to suggest that the spindles were responding to anything other than the origin-to-insertion length changes. However, the spindle model is accurate only for the linear, small-amplitude range, and so we investigated this issue further in acute reconstruction experiments (see later).

The reproducibility of the pattern of response described above is further demonstrated in Fig. 2, in which the data from six triceps surae Ia-afferents (two in soleus, four in gastrocnemius) are brought together. The plots show 30 superimposed and averaged paw-shake cycles comprising 5 cycles from each afferent. Instantaneous frequency from all cycles are overlayed, and a spike occurrence histogram is superimposed at the same frequency scale. Muscle length and EMG curves from each cycle are overlayed, and the resulting grand averages are superimposed. In both Figs. 1 and 2, it is clear that the bursts of Ia firing were temporally coupled to the bursts of lateral gastrocnemius EMG (bandwidth 100 Hz to 10 KHz, full-wave rectified and low-pass filtered: 40 dB/decade at 100 Hz), peak Ia firing preceding peak EMG by ~10 ms. It is also worth noting the very high Ia peak firing rates, typically 500–700 impulses/s (ips). It will be argued later that the peak net Ia input to the CNS during the paw-shake cycle is of the order 0.2 Mips, and the peak net Ia input from a single muscle such as soleus is of the order 20 Kips.

Responses of passive spindles to the reproduced length variations

Further confirmation that the Ia-afferents were essentially responding to the length variations as measured between muscle origin and insertion (length gauge tethered between ischium and tibia, ~1 cm distal to tibial tuberosity) was obtained in separate acute experiments performed on fully anesthetized cats (pentobarbital sodium, 40 mg/kg ip with iv maintenance doses). The aim was to reproduce accurately the length variations that had occurred in the awake animals in soleus muscles of the acute cats and to compare the responses of functionally deefferented Ia endings in the acute and chronic situations. The length variations recorded and digitized in 10 segments of paw shakes in 4 chronically recorded triceps surae Ia units were reproduced by an electromagnetic servo, pulling on the cut and freed tendon of the soleus muscle. Figure 3 shows the pooled time course of firing of 24 soleus Ia endings in such acute reconstruction experiments (*black dots*), superim-

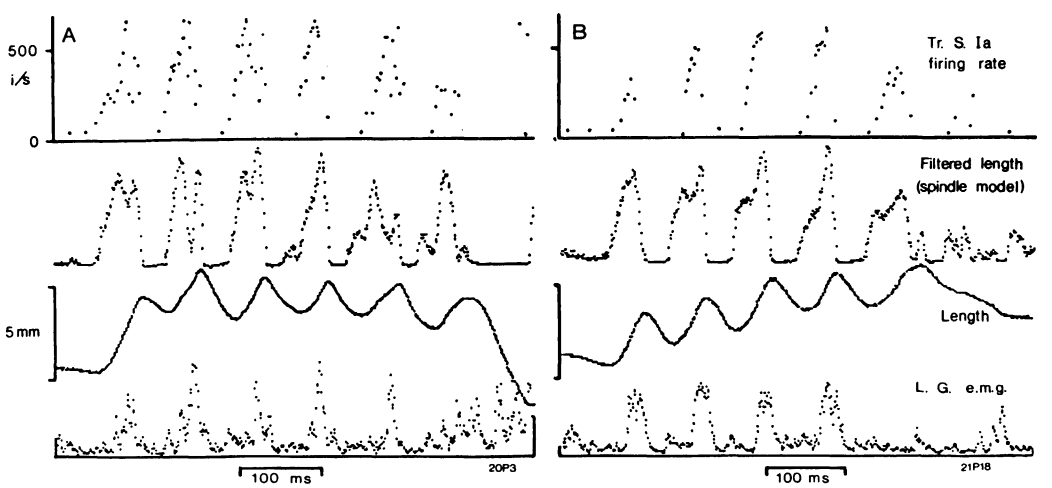

FIG. 1. Responses of two gastrocnemius spindle primary (Ia) endings during paw shakes in normal cats. *Top*: instantaneous Ia firing rates. *Middle*: responses of a linear Ia model (42) to reproduced versions of the origin-to-insertion muscle length shown in the third trace from top. *Bottom*: lateral gastrocnemius EMG. Note the high peak firing rates and the similar timing of the real and modeled responses in muscle lengthening.

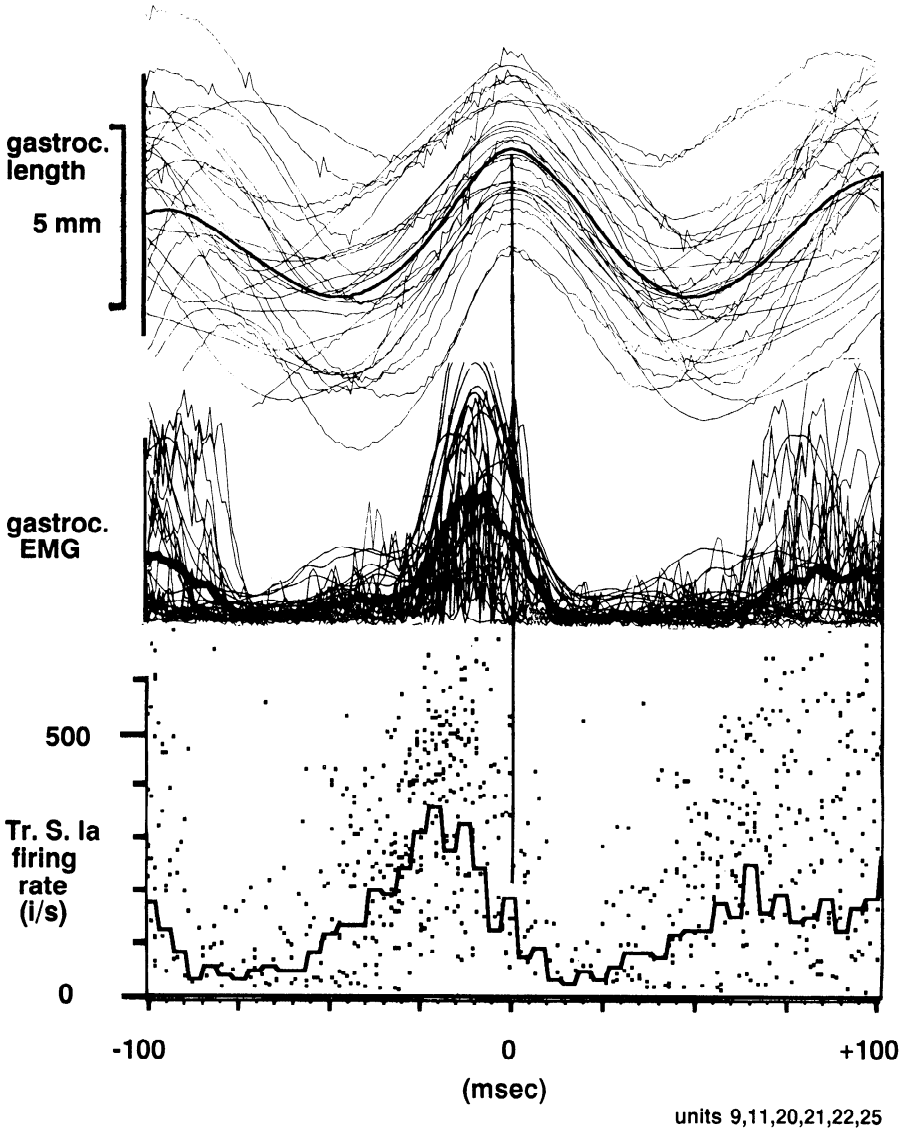

FIG. 2. Thirty superimposed and averaged paw-shake cycles from 6 Ia-afferents (each contributing 5 cycles). Cycles were aligned to the peak of lengthening. *Top*: superimposed length traces (light) and their mean (dark). *Middle*: superimposed EMG traces (light) and their mean (dark). *Bottom*: superimposed instantaneous frequencies (dots) and mean spike occurrence histogram (4-ms binwidth). Histogram was scaled to match the frequency calibration by averaging test sequences of known instantaneous frequency profile.

posed on the original chronic firing rate record (*grey dots*). The pooled profiles were obtained by computing the mean firing rates of the 24 afferents in corresponding 5-ms bins, each afferent contributing 5 complete response cycles to the pool (thus each grey-dot profile represents 120 cycles). The peaks in firing rate of the pooled Ia responses lagged slightly behind the corresponding peaks of the chronic Ia endings in the middle two or three cycles of the paw-shake sequences. The lag was coupled with substantial discrepancies in absolute firing frequencies. This is consistent with dynamic fusimotor action having been elevated at these times in the original recordings, as such action would both increase the amplitude and advance the phase of the responses to the large length changes involved (7). Further support for this interpretation was obtained in the simulation trials to be described below.

Simultaneity of triceps surae and hamstrings afferent firing

In view of the hypothesized difference in the role of proximal and distal muscles in the control of paw shakes (56), it was of some interest to study the response of hamstrings muscle afferents in such movements. Figure 4 shows the time course of firing rate of a spindle primary afferent and a tendon organ afferent, both from the posterior biceps/semitendinous muscle group, in two different cats. Two features relevant to issues raised in the INTRODUCTION are evident in these recordings. First, the timing and profile of the hamstrings Ia firing rate in relation to EMG and origin-to-insertion muscle length were very similar to those of the triceps surae Ia endings seen in Figs. 1–3. Again the phase relationship was consistent with the spindle effectively "seeing" the origin-to-insertion length. Second, the peak Ia firing rate exceeded 500 ips in most cycles, as it had in the triceps surae Ia endings. Indeed the efferent and afferent activity and the length variations of the proximal (hamstrings) and distal (triceps) muscles were virtually indistinguishable, even in absolute timing, as will be seen below. Second, the tendon organ (Ib) firing profile was surprisingly similar to that of the Ia ending, albeit there was a slightly smaller phase advance on muscle length (Fig. 4, *middle* record). Virtually identical relationships with Ia firing were observed in the two triceps surae Ib units recorded (not illustrated).

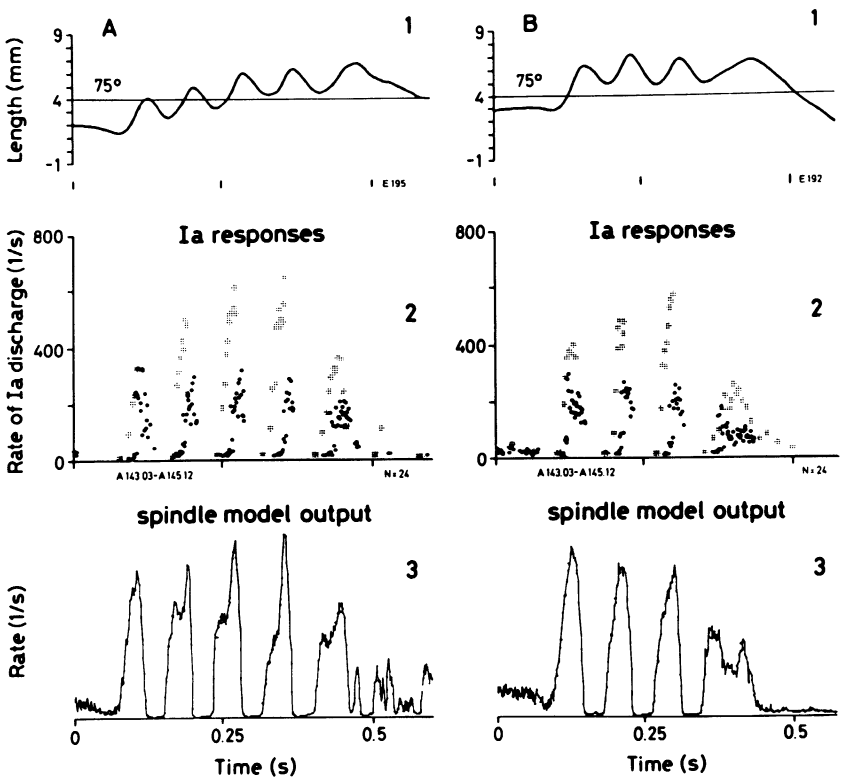

FIG. 3. Reconstruction of 2 paw-shake sequences whereby length variations recorded in the normal cat (*A1, B1*) were replicated in soleus muscle of 3 anesthetized cats. *A2* and *B2*: averaged-frequency responses of 24 passive Ia-afferents in the anesthetized cats (*black dots*) superimposed on the original responses (*grey dots*). For comparison, *A3* and *B3* show the responses of the linear spindle model (42) to length signals *A1* and *B1*.

We accidentally discovered that the length variations of hamstrings and gastrocnemius muscles may often be nearly in phase during paw shakes. In changing from the recording of a hamstrings to a triceps surae afferent, we initially changed the position of the length gauge but not the EMG connections. On replaying the data, we found

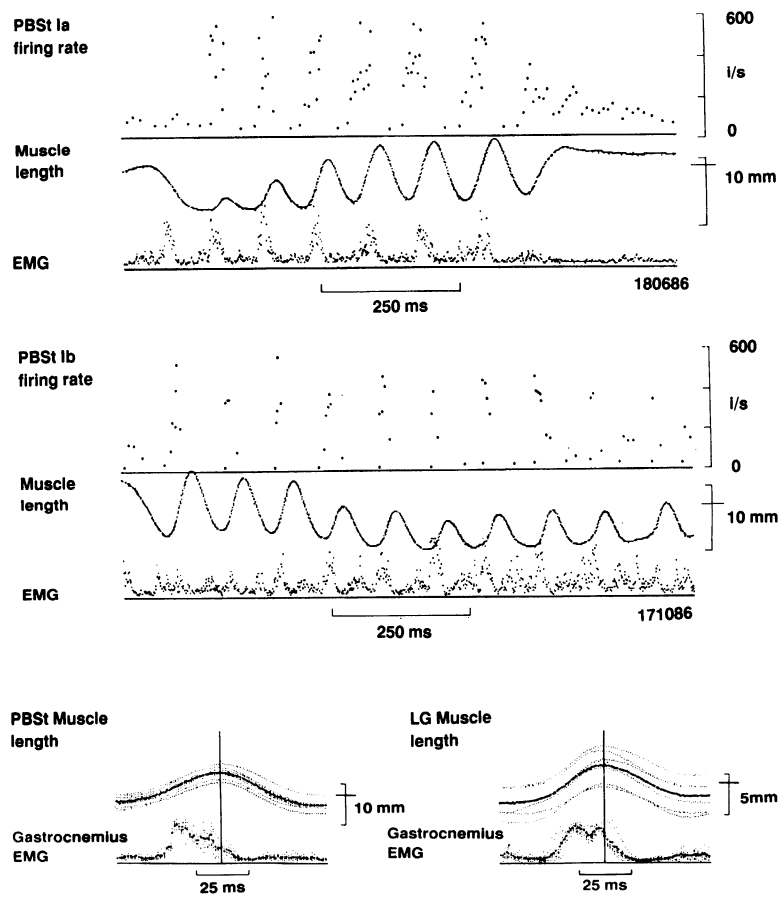

FIG. 4. Hamstrings involvement in paw shakes. *Top* and *middle panels*: responses of an Ia- and Ib-afferent, respectively, located in posterior biceps/semitendinosus (PBSt) during paw-shake sequences. The timing and peak firing rates of the Ia-afferent are similar to those of ankle extensor endings. The Ib-afferent is active toward the end of each stretch and reaches high peak firing rates. *Bottom panels*: superimposed (light) and averaged (dark) length and gastrocnemius EMG traces suggesting near simultaneity of hamstrings and gastrocnemius length variations in steady-state cycles. In both cases, alignment was to peak length.

that hamstrings and gastrocnemius length seemed to have a similar timing with respect to gastrocnemius EMG. This is illustrated in the lower records of Fig. 4, in each of which six paw-shake cycles are superimposed. The segments were aligned to the peak of length in each cycle. Given the low variability of coupling between EMG and length in these records, it follows that hamstrings and gastrocnemius length variations were virtually in phase.

We investigated this coupling further in two cats with simultaneous recordings of hamstrings and gastrocnemius muscle lengths (Fig. 5). In the paw-shake sequence of Fig. 5*A*, length oscillations of hamstrings and gastrocnemius started off in phase, but by the fourth cycle, hamstrings length was significantly advanced on that of gastrocnemius. The consistency of this pattern is seen in Fig. 5, *B* and *C*, in which cycle-by-cycle superimposition and averaging of the two length recordings was performed (*B*: 17 sequences in one cat; *C*: 5 in another). Cycles were aligned to hamstrings length maxima. Hamstrings reached peak length ~5–10 ms before gastrocnemius in the first three cycles. Asymmetries in the length profiles meant that hamstrings length minima were 20–30 ms advanced on those of gastrocnemius. In the fourth cycles, hamstrings developed a substantial phase lead on gastrocnemius and in the three cases where there was a fifth cycle, the average phase lead exceeded 180° (Fig. 5*B*).

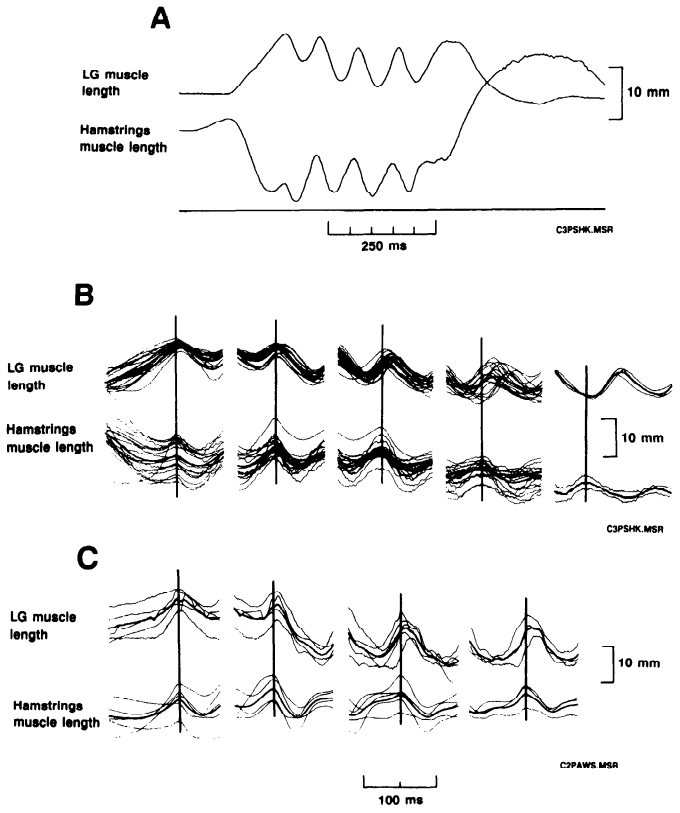

FIG. 5. Simultaneous recording of hamstrings and gastrocnemius length in 2 cats. *A*: single paw-shake sequence showing hamstrings and gastrocnemius to be virtually in phase for the first 3 cycles. *B*: cycle-by-cycle averages (*thick lines*) of 17 paw-shake sequences (from left to right: first cycle, second cycle, etc.) with superimposed single sweeps (*thin lines*). Cycles aligned to hamstrings length maxima. Note increasing phase lead of hamstrings on gastrocnemius in cycles 3–5. *C*: similar averages of 5 paw-shake sequences in another cat.

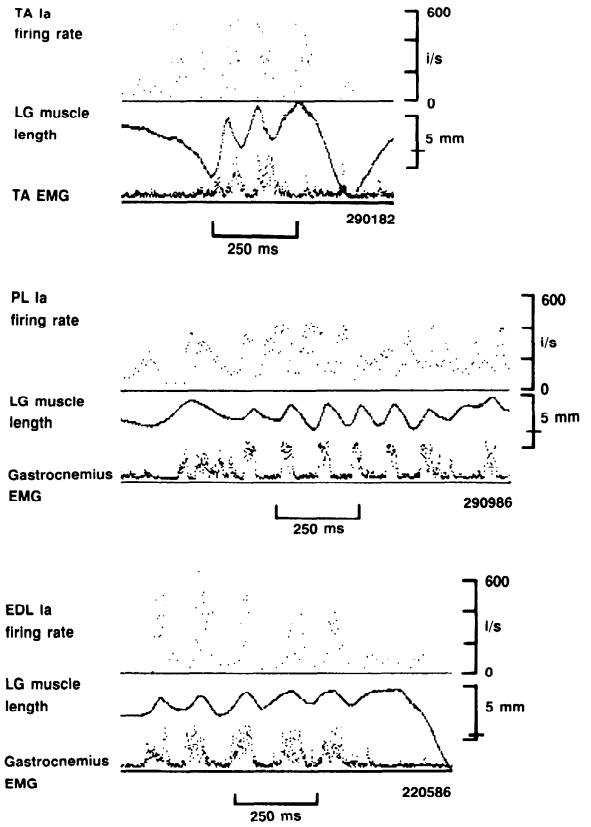

FIG. 6. Responses of tibialis anterior (TA, *top*), peroneus longus (PL, *middle*), and extensor digitorum longus (EDL, *bottom*) Ia-afferents in paw shakes. TA and EDL Ias reached peak rates during gastrocnemius shortening, in line with the presumed lengthening of their parent muscles. PL Ia had a more complex firing pattern, possibly reflecting its sensitivity to passively applied foot inversion.

Unloaded paw shakes: other afferents

In six spindle afferents (three plantaris, one peroneus longus, one tibialis anterior, and one anterior biceps femoris) fixation leads had not been implanted at the appropriate origin and/or insertion points. Figure 6 shows paw-shake responses in three such afferents, in relation to gastrocnemius length. The Ia-afferents in the foot dorsiflexors tibialis anterior and extensor digitorum longus (the latter also being a toe dorsiflexor) showed peak firing early in the gastrocnemius shortening phases (except tibialis anterior Ia, first cycle). The peroneus longus Ia-afferent was less well phase-locked to gastrocnemius length, possibly reflecting its sensitivity to foot inversion observed during the identification procedure. The peak firing rates in these three Ia-afferents were between 500 and 600 ips, which is similar to those of the other Ia afferents observed in this study.

Underlying fusimotor action

In acute experiments on eight separate fully anesthetized cats a total of eight paw-shake sequences selected from the stored chronic recordings of four triceps surae Ia endings were further studied with the aim of deducing the original

fusimotor action. As in the passive trials described above, the length variations that had occurred in the awake animals were reproduced accurately and cyclically in soleus muscles of the acute cats. Simultaneously, functionally isolated fusimotor filaments were stimulated to optimize the match between the responses of the acute and chronic Ia endings. This was achieved by a semiautomatic trial-and-error process whereby the time course of stimulus pulse frequencies was iteratively modified to produce the best match (26). Figure 7 shows the final outcome of two such reconstruction trials, in one case involving dynamic fusimotor (γ_d) stimulation only (*A*), and in the other, concomitant γ_d and static fusimotor (γ_s) stimulation.

The firing profile of the chronically recorded spindle Ia ending (Fig. 7*A: grey dots*) was matched well, both in phase and peak values of the acute spindle ending, by a time course of γ_d stimulation which started from a low level, "wound up" to a peak at the start of the penultimate stretch, and then abruptly declined. The addition of concomitant tonic γ_s stimulation (Fig. 7*B*) slightly improved the match in the short period before the paw shakes. Though the γ_d-dominated stimulus profiles shown were not unique in producing a good match (e.g., very deeply modulated stimulation of an exceptionally powerful γ_s filament did on one occasion give nearly as good a fit), they were by far the simplest and most general in giving good fits in paw-shake sequences of widely ranging time course. In all of our reconstructions so far, the salient feature has been the need for strong γ_d action, far in excess of that inferred for stance or gait, to produce the peak Ia firing rates characteristic of paw shakes. The reconstruction in Fig. 8 was typical of that obtained in six different Ia afferents in four separate acute experiments.

An interesting possibility suggested by the above results is that the CNS sets the gain around the stretch reflex arc so that the threshold of instability is exceeded. On this view, closed-loop parameters are scheduled, at the fusimotor and possibly other levels, to produce a well-defined period of limit-cycle instability, the outcome of which is a sequence of paw shakes. However, it has been shown that scratching (11) and paw shaking (33) persist after deafferentation. Furthermore, a doubling of paw mass did not significantly alter the duration of paw-shake cycles (23). The latter result is an important one for reflexology in general, and as it was obtained in chronic spinal cats, we were interested to see whether we could reproduce it in normal animals.

Paw shakes with weights attached to foot

In seven cats, cuffs comprising thin 35-mm-wide strips of lead were wrapped around the paw just proximal to the metatarsophalangeal joint and fastened in place by Velcro.

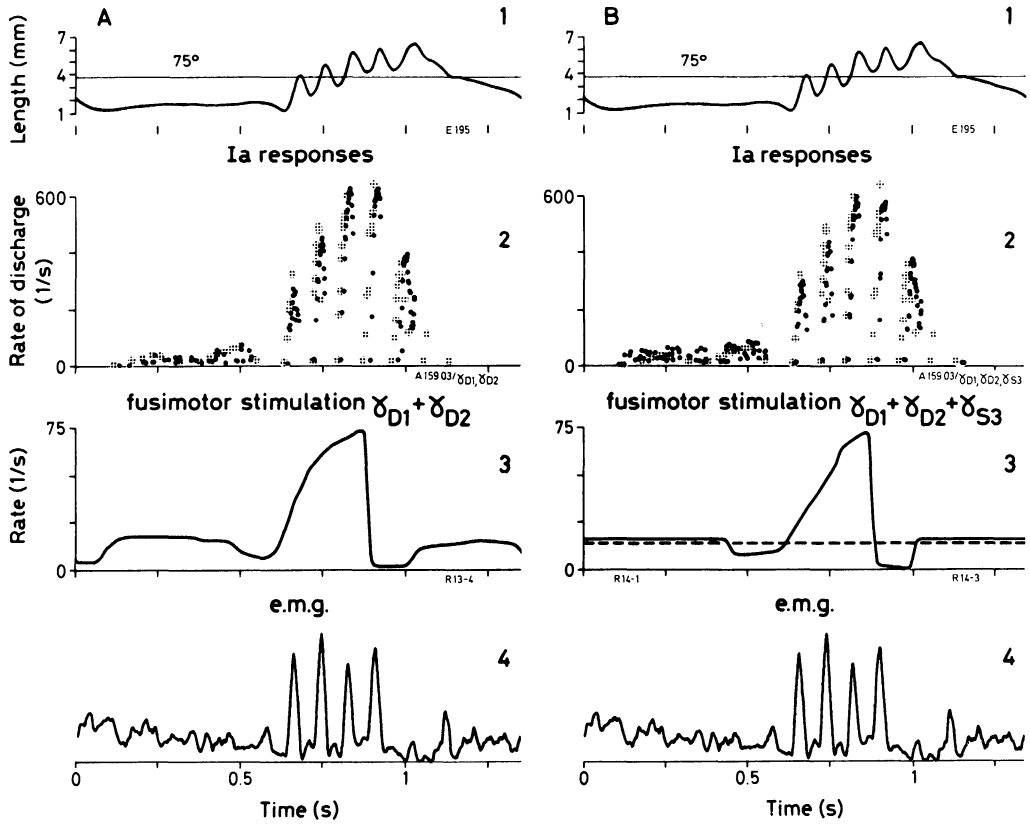

FIG. 7. Reconstruction experiments involving controlled fusimotor stimulation. The chronically recorded length profile (*A1* and *B1*) was applied to a soleus muscle in an anesthetized cat. Responses of a test Ia-afferent (*black dots*) were made to match the original Ia responses in the normal cat (*grey dots*) by an iterative optimization of fusimotor stimulation (*A3* and *B3*). *A3*: 2 single dynamic fusimotor fibers were together stimulated with the pulse rate profile shown. *B3*: separate static fusimotor stimulation (*dashed line*) was added. In *A3* and *B3*, the waxing and waning profile of dynamic fusimotor action was required to achieve a good match. *A4* and *B4*: original gastrocnemius EMG.

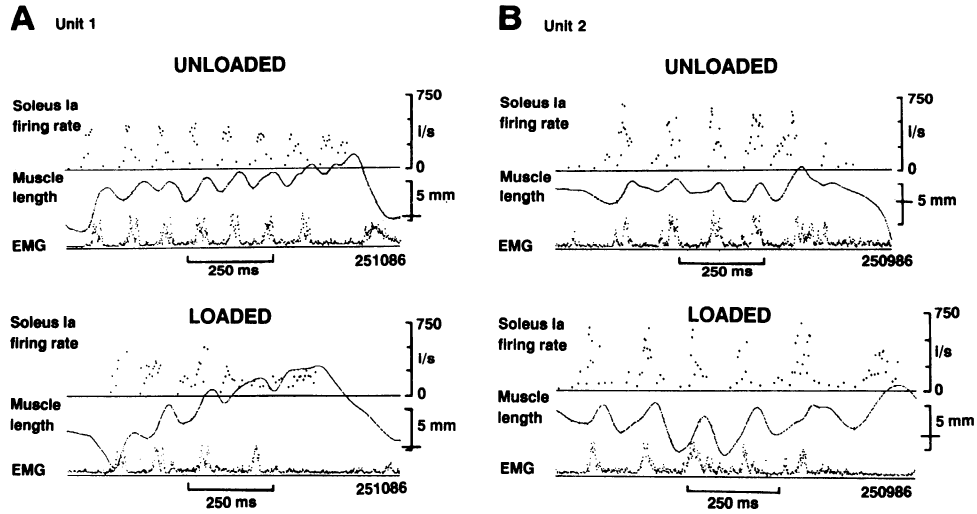

FIG. 8. Paw shakes with inertial loading. Responses of 2 soleus Ia endings (*left* and *right*, respectively). *Top*: no load; *bottom*: inertia of foot approximately doubled by lead cuff. Mean frequency of the loaded paw shakes reduced, but the timing of Ia responses with respect to origin-to-insertion muscle length was not significantly changed (most firing occurred during stretch in all 4 cases).

Care was taken to mold the cuff to the contours of the foot so that relative movement between the two during paw shakes would be minimized. Three cuffs (42, 46, and 47 gm) were used either singly, or in pairs, with the second wrapped over the first. The moments of inertia of the cuffs calculated on the basis of distance from the estimated pivot point at the ankle were 0.099, 0.109, and 0.111 $g \cdot m^2$, respectively. In one cat, the foot was disarticulated post-mortem and weighed (27 g). Its moment of inertia about the ankle, assuming a linear mass distribution, was 0.08 $g \cdot m^2$. Thus single cuffs increased the net moment of inertia by up to a factor of 2.4, and double cuffs increased it by up to a factor of 3.6.

Cats adjusted to the presence of the cuffs quickly. Within a minute or so of attachment, the loads were virtually disregarded, and the only enduring differences in gait were

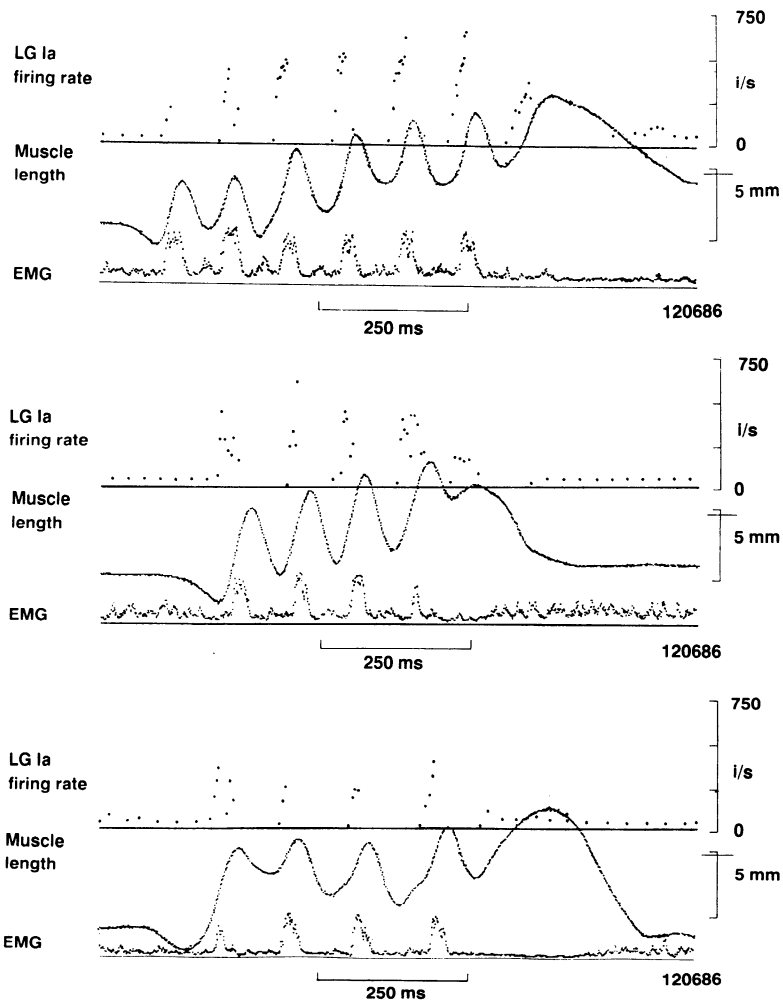

FIG. 9. Paw shakes with inertial loading. Responses of a gastrocnemius Ia-afferent. *Top*: no load; *middle*: 1 lead cuff, approximately doubling foot inertia; *bottom*: 2 cuffs, approximately tripling inertia. The timing of the Ia responses with respect to origin-to-insertion muscle length remained similar, and there was no evidence of a phase reversal even with the highest load.

TABLE 1. *Individual mean periods of single paw-shake cycles*

	No Weight	1 Weight, 46 g	2 Weights, 93 g
First cycle, ms	84 ± 7 (20)*	115 ± 9 (18)*	115 ± 10 (14)†
Second cycle, ms	89 ± 6 (20)*	122 ± 11 (17)*	126 ± 9 (13)†
Third cycle, ms	89 ± 5 (18)*	117 ± 13 (12)*	109 ± 9 (7)†
Fourth cycle, ms	92 ± 2 (14)*	147 (1)	119 ± 27 (2)‡
Grand mean	88 ± 3 (16)	118 ± 6 (13)	117 ± 6 (11)
Equiv freq	11.4 Hz	8.5 Hz	8.5 Hz

Values are means ± SE; numbers in parentheses are no. of cycles. *4 cats, each mean from 2–5 cycles. †3 cats, each mean from 1–5 cycles. ‡2 cats.

a tendency for hyperflexion to be evident in the swing phase, and the occasional intercalated paw-shaking sequence to occur. The paw shakes themselves were, however, less regular. With double cuffs, apparent attempts at initiating sustained paw shakes were often aborted after one or two cycles. Significant inversion and eversion was noted at the ankle for the heavier loads.

Figure 8 shows the firing of two soleus Ia endings recorded during paw shakes with and without a single cuff attached to the paw. In both spindles, loading resulted in movements of a slightly lower frequency (*A*: 11.6 Hz unloaded, 8.9 Hz loaded; *B*: 8.8 Hz unloaded, 7.9 Hz loaded), but the phase relationship between spindle firing and origin-to-insertion muscle length was not appreciably affected.

Figure 9 shows similar effects in a lateral gastrocnemius Ia ending during paw shakes in three conditions: unloaded, one cuff (46 g), and two cuffs (93 g). Loading reduced both the regularity and the mean frequencies of the movements (11.4, 11.1, and 9.3 Hz, respectively). Again, the timing of the spindle discharge relative to the origin-to-insertion length changes was relatively constant.

Table 1 shows results collated from four cats. For each cat, we chose maximally five paw-shake sequences in each of three loading conditions (unloaded, one weight, and two weights). Each cycle period was measured and grouped according to its order in a sequence and to the loading condition. The mean of each group (e.g., *cat 1*, one weight, 5-s cycles) was now calculated. The means of these means are shown in the table, along with estimates of the standard errors. The grand means (±SE) are simply those of the means in each column (i.e., each loading condition). We chose not to compute grand means and standard deviations of single cycles from different cats because there was no guarantee that these were from a single distribution. The equivalent frequencies correspond to the inverse of each grand mean.

Inertial loading reduced the numbers of cycles per sequence. The results were unequivocal in showing that loading consistently increased the mean cycle durations. However, there were no significant differences between trials with single and double weights.

DISCUSSION

Peak firing rates of proprioceptors

A central finding in this study was that muscle spindle and tendon organ afferents reached very high peak firing rates (400–700 ips) during the phase of the paw-shake cycle in which the parent muscle lengthened. During shortening they fired little or silenced completely. The generality of this pattern is evident in Fig. 2, which shows the ensemble firing of six triceps surae Ia afferents. Ia discharge was displayed both as a frequencygram and an event occurrence histogram for 30 cycles aligned at peak muscle length. The two modes of presentation give very different impressions of firing rate, because the absences of events in a bin are given equal weight with occurrences in the histogram, whereas occurrences only are registered in the frequencygram. It is not immediately obvious which of the two presentations is more meaningful. The frequencygram reveals a large variation in instantaneous firing rate which is due partly to the variability of successive interspike intervals in individual afferents and partly to systematic differences between afferents in onset and peak of firing. This variability is largely smoothed out in the histogram, yet it may be important physiologically because short interspike intervals are known to potentiate Ia transmission at motoneuronal synapses (10). On the other hand, the total number of impulses per unit time is accurately represented by the histogram, whereas a curve of best fit drawn through the frequencygram would lead to considerable overestimates of mean impulse frequency. Note that a third mode of presentation, the averaged-frequency histogram, was used in Fig. 3. In this, the instantaneous firing rates in corresponding bins are averaged. This preserves transients more than the event occurrence histogram, while emphasizing sporadic high-frequency events less than the frequencygram.

The peak mean Ia firing rate from the histogram is ~350 ips, though all six contributing afferents individually exceeded 500 ips peak rates in most cycles. As evidenced in Figs. 1, 4, and 6, similar peak firing rates were observed in all the Ia afferents in our sample, irrespective of the receptor bearing muscle. This uniformity allows estimates to be made of overall peak inputs to the spinal cord from single muscles, as well as from groups of muscles whose length variations are in phase during paw shaking. Medial gastrocnemius is innervated by some 60 Ia afferents (8). Thus the peak net Ia firing from this muscle is ~21 Kips (60 × 350). Lateral gastrocnemius, with ~35 Ia afferents, would give rise to ~12 Kips maximal net Ia firing. Values for some other major hindlimb muscles are as follows: soleus [~56 Ias (8)]: 20 Kips; semitendinosus [~120 Ias (5, 8)]: 42 Kips; tibialis anterior [~71 Ias (8)]: 25 Kips; rectus femoris [ca. 62 Ias (5)]: 22 Kips.

EXPECTED SYNAPTIC ACTION. On average then, the large hindlimb muscles each generate ~20 Kips peak net Ia firing in each paw-shake cycle. It has been estimated that 14 Kips of Ia input would bring motoneurons to threshold from rest, and 20 Kips would be required to produce maintained discharge (31). These estimates were initially derived for intercostal motoneurons, but it was later argued that the overall average EPSP amplitude in hindlimb muscles is virtually identical (30). On the basis of 80–90% connectivity (a given motoneuron is contacted by 80–90% of all homonymous Ia-afferents; Refs. 17, 37, and 39) homonymous Ia input of 16–18 Kips might just suffice to cause reflex activation of motoneurons *if no other excitatory or*

inhibitory inputs were involved. To this input must be added the Ia contribution from synergistic muscles. For example, in medial gastrocnemius motoneurons, connectivity from lateral gastrocnemius and soleus Ia afferents is reported at 49 and 42%, respectively (52). When combined with the estimated peak net Ia rates of 12 Kips (lateral gastrocnemius) and 19 Kips (soleus), this would add the equivalent of 14 Kips. A further small contribution would arise from plantaris (13) which, on the basis of our data from three spindle afferents, lengthens and shortens in phase with medial gastrocnemius. According to our estimates then, the total peak monosynaptic input from Ia afferents to the average medial gastrocnemius motoneuron is therefore 30–32 Kips.

MOTOR OUTCOME. The peak Ia firing rates of Fig. 2 are similar to those mediating tendon jerk responses in the conscious cat (49). Furthermore, Fig. 2 shows that the ensemble triceps Ia input leads gastrocnemius EMG by ~10 ms or tendon jerk latency (49). It is therefore reasonable to suppose that the Ia input assists in the generation of the EMG bursts. But the EMG bursts reflect the commands which *cause* the paw shakes and indeed make them grow in amplitude in the first few cycles. The phase lead of EMG on movement is consistent with the load-moving properties of muscle (42) and explains why a Ia-mediated stretch reflex would assist rather than resist the oscillations (48). In humans this can be readily demonstrated by exciting Ia-afferents during the stretch phase of a tremor (48).

From all the above, it is tempting to conclude that in paw shakes the gain in the monosynaptic reflex arc exceeds the threshold for instability and that the paw shakes themselves are simply limit-cycle oscillations in an unstable feedback loop. However, various factors militate against this oversimplified view. First, there is an unknown amount of concomitant inhibition, presynaptic as well as postsynaptic. The tendon organs in our sample reached peak firing rates at nearly the same time as homonymous spindle afferents. In some motoneuron pools this input might produce enough inhibition to reduce the peak net excitation to below threshold levels. Reciprocal inhibition would probably be minimal in this respect because of the reciprocity of the Ia activation patterns.

Second, in paw shakes there is phase-coupling of the activation of muscles in the entire limb (see below). Autonomous reflexive oscillators at the hip, knee, and ankle would not produce this linked pattern. On the other hand, if all of the oscillators (including the putative "central pattern generator") had similar natural frequencies, they could be pulled into synchrony by the dominant oscillator, depending on how sharply they were "tuned" (40, 41, 58). Impedance analysis suggests that the tuning of reflexly active extremities tends to be broad both in soleus of the decerebrate cat (Fig. 5 in Ref. 28) and at the human elbow joint (Fig. 5 in Ref.; Ref. 48).

Third, rhythmical motor activity, though at frequencies lower than those of paw shakes, can be elicited in chronic spinal deafferented cats by stimuli which evoke paw shakes prior to deafferentation (33). It seems likely that the central oscillator thus revealed would be active in normal paw shakes, and would interact with the peripherally mediated oscillators as discussed above, either in a dominant or entrained form.

ENSEMBLE INPUT FROM LIMB. A further deduction may be made about peak ensemble Ia firing rates. In early paw-shake cycles (see below), hamstrings and triceps surae muscles lengthen at virtually the same time. If we assume similar peak net Ia firing rates in gracilis and biceps femoris as estimated above for semitendinosus (42 Kips), and add the total (126 Kips) to the total for triceps surae and plantaris (e.g., 70 Kips), a grand total of nearly 200 Kips (0.2 Mips) is obtained. This is almost certainly an underestimate of the peak net Ia input to the spinal cord, as the pure hip extensors (gluteus medius, anterior biceps femoris, and semimembranosus) are probably stretched at the same time as the biarticulate hamstrings muscles (55), and flexor digitorum longus and flexor hallucis longus are likewise probably stretched in phase with triceps surae. In addition to the major muscles named above, there are numerous smaller muscles of the hip, leg, and foot which would contribute further Ia input.

Coupling of hamstrings and triceps surae length changes

In their elegant study of coordination in paw shakes, Smith et al. (56) described three distinct phases of a typical paw-shake sequence: *start-up*, comprising the initial 4–6 cycles during which hip, knee, and ankle actions become organized; *steady-state*, the middle 3–5 cycles characterized by consistent displacement at all three joints; and *slow-down*, the last 3–4 cycles during which joint excursions decrease and slow. In our data, there were generally fewer than 9 cycles per sequence. This may be because the paw shakes often occurred during gait rather than stance (6). In the two animals in which we recorded hamstrings and gastrocnemius length simultaneously, we observed progressive changes in relative timing of muscle displacement consistent with the above description (Fig. 5). In early cycles, peak stretch velocities occurred almost simultaneously in the hamstrings and ankle extensor muscles. Phase-slip developed in the final cycle or two of a sequence.

The objective of paw shakes is evidently to dislodge matter adhering to the foot, and this would best be achieved by maximizing paw accelerations. The progressive phase lead of hamstrings over the ankle extensors raises the question of how end-point accelerations vary with increasing phase differences between joints. The whiplash effect of delaying movements of the wrist with respect to movements of the shoulder and elbow is well-known to musicians and sportspeople alike, but curiously physiologists have not analyzed the kinematics of such strategies, nor have they identified the situations in which they are advantageous.

Underlying fusimotor action: generalized increase in reflex transmission?

In many, though not all paw-shake sequences, there was evidence of a waxing and waning Ia sensitivity. Often, the responses to the first and last muscle stretches in a sequence were substantially lower than to the rest, as judged by comparisons with responses to identical length signals of functionally deefferented spindles and the spindle model (Figs.

3 and 1, respectively). In the more rigorous reconstruction experiments of the type illustrated in Fig. 7, it emerged very clearly that a large surge in dynamic fusimotor (γ_d) action was the only realistic explanation for the very high peak Ia firing rates we observed in paw shakes. This is interesting both for the light it sheds on fusimotor control in general, and also for the implication that in paw shakes the CNS "chooses" to wind up the gain in the stretch reflex arc.

Elevated γ_d action has previously been implicated when movements were imposed on animals, a situation in which vigilance was assumed to be raised (47). The term "fusimotor set" was invoked to describe the mechanism underlying such transitions in fusimotor action. It was hypothesized that at rest or in routine tasks such as stance and locomotion, fusimotor action is set to low levels (though cf. Refs. 38 and 60), whereas in novel, difficult, or strenuous tasks, fusimotion, particularly of the γ_d type, was increased. Other workers have also speculated upon the control of *dynamic* fusimotor neurons separately from α-motoneurons (2, 3), and Greer and Stein (1986) have recently shown that in the cat intercostal muscles, dynamic fusimotor action was recruited when respiratory drive was experimentally increased.

A weakness in the original fusimotor set proposal was that it was based largely on studies of three specific situations: rest, gait, and imposed movements. Of late, we have obtained evidence that fusimotor resetting can also occur in difficult beam-walking tasks and after sudden, large postural perturbations (46). The present data allow us to add paw shakes to the growing list of situations in which elevated fusimotor set is consistently detected.

One could also speculate on why the CNS increases Ia sensitivity in paw shakes. A possibility discussed above is that reflexes are intentionally made unstable and become integral parts of the neural generator of paw shakes. But augmenting Ia sensitivities is not the only way to augment reflex loop gain. If destabilization is indeed the aim, one might predict concomitant reductions in presynaptic inhibition. Polysynaptic transmission via both segmental and "long-loop" pathways might be elevated. Ia synaptic transmission may be significantly potentiated by the pattern of high-frequency Ia bursts (10). These central mechanisms could be sought by monosynaptic testing in "fictive" motor preparations, provided that convincing paw-shake-like activity patterns could be elicited.

Effect of inertial loading

Two clear results emerged from trials in which weights were attached to the foot. First, the relationship between origin-to-insertion muscle length and spindle afferent firing during paw shakes was little affected by doubling or even tripling the moment of inertia of the foot. Second, such loading was associated with significantly reduced mean paw-shake frequencies.

Recently there has been some debate about whether tendon stretch contributes significantly to origin-to-insertion displacement in active contractions (1, 14, 15, 21, 24). In principle, when activated, muscle fiber compartments could become stiffer than the tendinous compartments in series with them. Depending on the load, spindles in the muscle compartments would then "see" mechanically filtered versions of the origin-to-insertion displacement. For example, in rapid tremor (or paw shakes), if the natural frequency of the tendon and the inertial load presented by the extremity were exceeded, a phase reversal between internal and origin-to-insertion muscle displacement would occur. Indeed with doublets of electrical stimulation alternating between agonists and antagonists, such phase reversals have been detected in human arm muscles (14, 15).

There was no evidence of phase reversal between spindle firing and origin-to-insertion displacement in our study, even when large loads were added to the foot. Indeed the timing of the responses with respect to length was quite closely matched both by the electronic model and Ia endings in inactive muscle, when the original length variations were reproduced. It could still be argued that mechanical phase reversals were actually present in the active muscles, but that phasic fusimotor activity was reprogrammed to compensate exactly for the different loading conditions. We would reject this possibility on the grounds that fusimotor action, no matter how deeply modulated, would be unlikely to produce the maximal Ia firing rates observed *if the spindles were shortening* (4). In Fig. 9, and to a lesser extent in Fig. 8, there is a reduction in peak Ia response frequencies with loading. This is suggestive of a reduction in internal muscle displacement. However, loading was also associated with lower peak muscle velocities, which would account for some if not all of the decline in Ia response. Furthermore, there is no guarantee that fusimotor set was constant throughout. We therefore feel that though it is safe to reject the occurrence of complete phase reversals, the possibility of reductions in internal displacement with heavy loading cannot be resolved one way or the other with our data.

Though the muscle and limb velocities attained in paw shakes are probably among the largest of which the animals are capable, it does not necessarily follow that the muscle forces are also maximal. Peak torque about the ankle during paw shakes has been estimated at ~0.5 Nm (25). In quiet stance, ankle torque in a 3-kg cat would be ~0.5–0.7 Nm (7.5–10 N at paw, perpendicular to axis of foot, moment arm 70 mm). Doubling the inertia of the foot might have doubled the peak torque if paw-shake frequency had remained constant (peak torque = 0.69 × moment of inertia × frequency^2). However, frequency declined on average by ~25%, so peak torque is unlikely to have risen by >20–30%. If these various estimates are reasonably accurate, one reaches the surprising conclusion that peak muscle forces during paw shakes are in fact at the lower end of the physiological range and comparable to those in quiet stance. Even so, without the empirical evidence above, one could not have ruled out significant tendon displacement in paw shakes since tendon compliance is highest at low force levels (51). Our conclusion regarding tendon strain cannot safely be generalized to movements involving much larger force variations, such as trotting, running, and jumping. Here the issue remains open and awaits further direct evidence.

REDUCED FREQUENCY. The reduction in paw-shake frequency seen both in the displacement and in the EMG,

with doubling or tripling of foot inertia supports a reflex-based generation of paw shakes rather than a central pattern generation. Increased inertia would lower both the mechanical resonant frequency of the muscle/load and the bandwidth of the load-moving muscle (42), which would reduce the frequencies of reflex-mediated oscillations, whereas purely centrally generated oscillations would be unaffected. The large modulation of Ia input discussed earlier, and its timing with respect to homonymous EMG lends support to a reflex-based mechanism. Yet this mechanism alone cannot account for our observation that the reduction in paw-shake frequency caused by one weight was not augmented by the addition of a second similar weight.

Many variables are involved which might contribute to changes in paw-shake frequency. The detection of a load by the higher centers might cause parametric adjustments of the central pattern generator and of reflex pathways, altering paw-shake characteristics. A generalized resetting of this sort is certainly supported by the observation that loading reduced the number of paw shakes per sequence, drastically so in the two-weight condition. Background coactivation of antagonist muscles might occur with the larger weights and this might offset the frequency reductions expected from mechanical properties alone. It is of interest in this context that in chronic spinal cats, inertial loading markedly reduced paw-shake frequencies for loads > 3 times paw mass (23: Fig. 1).

From all of the above it is clear that peripheral input is closely involved in determining the characteristics of paw-shake sequences. It is also clear that the spinal central pattern generator can initiate and sustain paw-shake-like sequences, albeit at lowered frequencies, without afferent input (33). Koshland and Smith (33) have suggested that spinal networks set minimal criteria, whereas hindlimb afference modifies the temporal structure of successive cycles. This is similar to our notion that central and peripheral pathways, including the muscle/load should be viewed as inextricably linked components of the pattern generator for this class of movement (12).

NOTE ADDED IN PROOF

In a recent study (17), forces in soleus and medial gastrocnemius tendons were monitored during paw shakes in two conscious cats. Mean peak forces were measured as 5.7 N (gastrocnemius) and 0.6 N (soleus) in one cat and 28 N (gastrocnemius) and 2.4 N (soleus) in the other. Walmsley et al. (61) reported medial gastrocnemius forces of ~5 N in stance and 10 N in walking and running. Twenty newtons was only exceeded in jumping. Soleus forces were ~12 N in stance and 15 N in walking. The peak gastrocnemius forces reported by Fowler et al. (17) are very different in their two cats, one peak corresponding to tonic force in quiet stance, the other exceeding peak force in fast running. Soleus forces in paw shakes were below those in quiet stance in both animals. Thus tendon compliance effects (e.g., phase reversals) should be more evident in gastrocnemius Ia-afferents but not in soleus Ia-afferents. Figure 2 comprises four gastrocnemius Ia-afferents and two soleus Ia-afferents, and there was no detectable phase difference between them.

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