

The distal hindlimb musculature of the cat

Patterns of normal use

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Summary. Chronic recordings were made of electromyographic (EMG) activity, tension, and length of distal hindlimb muscles in six cats performing a variety of normal motor tasks. Muscles studied thoroughly or in part were medial gastrocnemius, lateral gastrocnemius, plantaris, soleus, flexor digitorum brevis, flexor digitorum longus, flexor hallucis longus, tibialis posterior, tibialis anterior, extensor digitorum longus, peroneus longus, and peroneus brevis. Postural and locomotor activities were examined, as well as jumping, landing, scratching, and paw shaking. In general, muscles could be assigned to traditional groupings (e.g. extensor, flexor) related to the demands of the motor task. Patterns of muscle activity were most often consistent with current understanding of muscle mechanics and neural coordination. However, purely functional distinctions between flexor digitorum longus and flexor hallucis longus ("anatomical synergists") were made on the basis of activity patterns. Likewise, the activity of plantaris and flexor digitorum brevis, which are attached in series, was differentiated in certain tasks. The rhythmical oscillatory patterns of scratching and paw shaking were found to differ temporally in a manner consistent with the limb mechanics. In several cases, mechanical explanations of specific muscle activity required length and force records, as well as EMG patterns. Future efforts to study motor patterns should incorporate information about the relationships between muscle activation, tension, length and velocity.

Key words: Muscles - Locomotion - Kinesiology - Electromyography

Introduction

A systematic understanding of motor control requires detailed information about the interaction of constituent elements. Data have been gathered on mechanical and structural characteristics of individual muscles (e.g., Sacks and Roy 1982; Goslow et al. 1972, Spector et al. 1980) as well as kinematic and kinetic characteristics of limb movement (Arshavskii et al. 1965; Orlovskii and Shik 1965; Engberg and Lundberg 1969; Goslow et al. 1973; Wetzel et al. 1976; Tokuriki 1973a, b, 1974; Manter 1938). Neurophysiological investigations in acute preparations continue to reveal properties of particular motoneuron pools (e.g., Dum et al. 1980; McDonagh et al. 1980). However, interpretation of these data with respect to the neural bases of behavior requires information about the participation of these muscles and motoneuron pools in a variety of behaviors.

Recent advances in chronic recording techniques have made possible the acquisition of muscle dynamics (force and length) data, together with well delineated electromyographic (EMG) records, during reflexly and voluntarily controlled behaviors of intact animals (Prochazka et al. 1974; Walmsley et al. 1978; O'Donovan et al. 1982; Loeb et al. 1980). In this study, most of the major muscles in the cat distal hindlimb were monitored simultaneously, providing information about the actions and interactions of these muscles during standing, walking, trotting, jumping, landing, scratching, and paw-shaking. This information provides some new insights into issues of motor control such as the relationships among muscle activation, length change, and force production. In addition, this information may serve as a basis for developing dynamic models of real motor control systems. A preliminary report of some of these data has appeared previously (Abraham et al. 1981).

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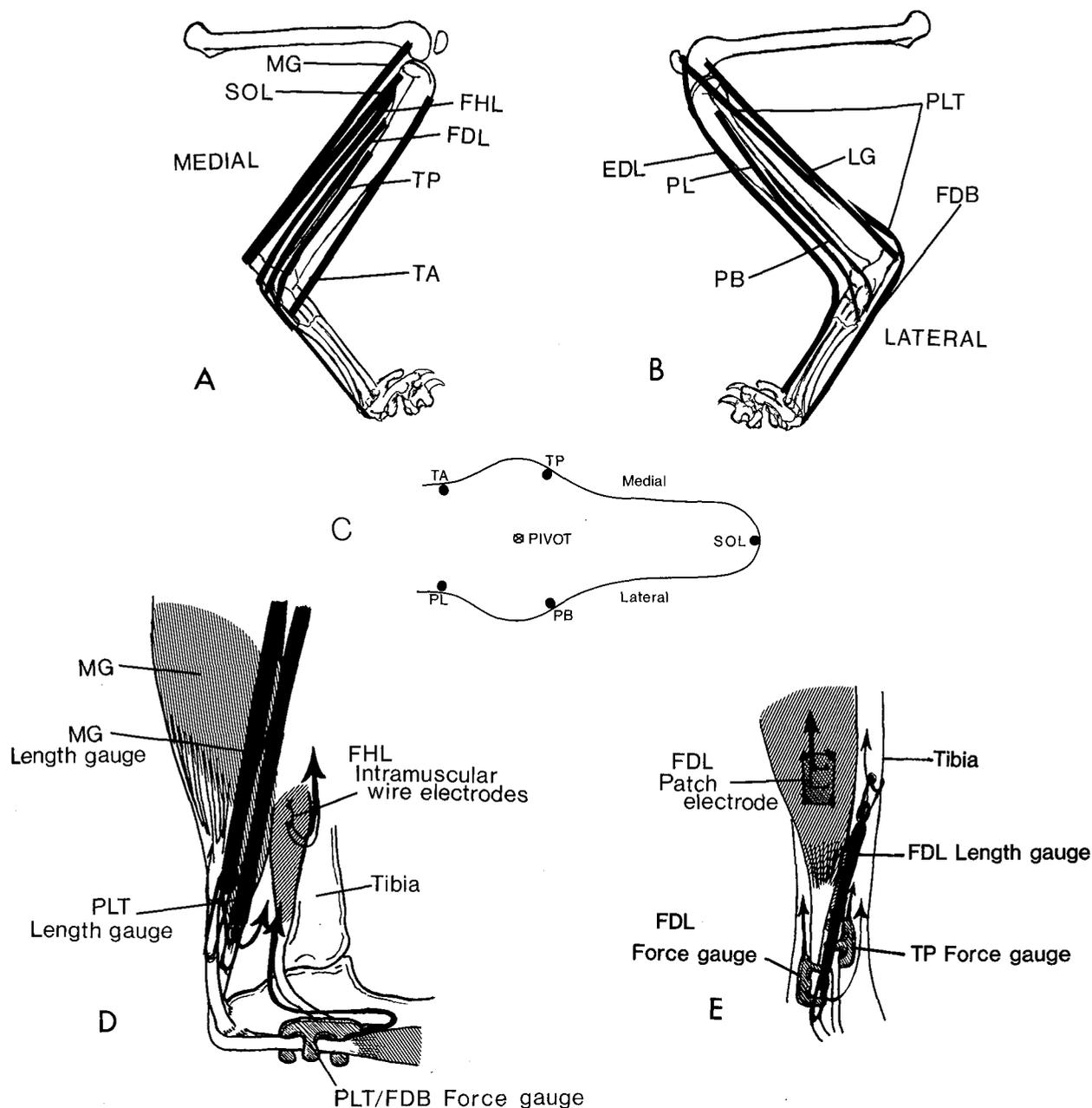


Fig. 1. A and B Medial and lateral schematic views of muscle attachments; C Schematic (top) view of muscle attachments to foot relative to the ankle joint; D and E Sample implanted device locations (arrows show wire paths toward backpack connector)

Methods

One female and five male cats were used (3.0–4.5 kg). All animals were trained daily for several weeks prior to surgery to walk and trot at a regular pace on a treadmill and to tolerate various manipulations of the left hindlimb. Training was also provided in jumping and (for one cat) standing with each paw on a separate load-transducing pedestal. Electromyographic recordings were taken from seven to eleven muscles in each cat, surveying a total of twelve muscles: posterior (extensor) compartment – medial gastrocnemius (MG), lateral gastrocnemius (LG), plantaris (PLT), soleus (SOL), and flexor digitorum brevis (FDB); the deep medial

compartment – flexor digitorum longus (FDL), flexor hallucis longus (FHL), and tibialis posterior (TP); the anterior compartment – tibialis anterior (TA) and extensor digitorum longus (EDL); and two of the peroneals – peroneus longus (PL) and peroneus brevis (PB) (See Table and Figs. 1A and B). The attachments of these muscles to the foot of the cat provide five major types of action at the ankle joint (Fig. 1C). Length gauges were used to provide records of joint position (ankle and, in a few cats, knee) as well as the particular length of one or two muscles in each cat. One or two tendon force transducers per animal were used as has been described previously (O'Donovan et al. 1982; Loeb et al. 1980; Walmsley et al. 1978).

All of the behaviors described here were observed in five or six different preparations except for dropping (two) and standing on force plates (one). The records shown here were selected and arranged by the following criteria from the different combinations of signals available in each preparation:

1) Completeness – We have selected, when possible, groups of records that show the EMG, length, and tension of a particular muscle and/or its synergists.

2) Contrast – We have juxtaposed certain muscles where particular patterns of synergy or antagonism are evident from the precise temporal relationships of activity.

3) Repeatability – We have selected records that were most typical of patterns seen repeatedly and across animals, rejecting occasional anomalous records seen rarely or in only one preparation which may have been due to defects in the performance or location of an implanted device.

4) Cleanness – We have selected traces that were least affected by occasional sources of electrical artefact, such as line noise, motion artefact, pick-up of transducer excitation signals, and connector noise. Minor amounts of such interference usually degraded the records of 1–3 channels in each preparation, although not to an extent that compromised determination of the natural activity patterns of the muscle. In a few preparations, one or two channels were unusable due to noisy signals, usually caused by broken leads, which were easily identified during routine impedance testing of all implanted devices prior to recording sessions.

Device implantation

All recording devices were implanted during an aseptic surgical procedure. Anesthesia was maintained intravenously with barbiturate (30 mg/kg i.p. Nembutal, initial dose); pre- and post-operative doses of antibiotic (cephalothin, 100 mg) were routinely administered. Within 8–20 h after the end of surgery the animals were sufficiently recovered to be removed from the temperature- and humidity-controlled recovery chamber and returned to their home cages. Most animals resumed semi-normal use of the operated hindlimb within three to four days, and all were walking without noticeable limp after ten days.

EMG electrodes

The EMG activity of individual muscles was recorded using bipolar stainless steel wires. For a few large muscles (e.g. MG, LG), exposed tips of Teflon-insulated, stranded wires (Bergen Wire Rope, BWR 3.48) were buried in the belly of the muscle and the wires sutured in place to the overlying fascia. The exposed recording surfaces were 2–3 mm in length and about 4 mm apart. This technique, however, is less suitable for small muscles, as the proportion of the muscle damaged by the implantation increases, as does the electrical crosstalk from adjacent muscles. Therefore, most EMG records were obtained using “patch” electrodes which consisted of short (3–4 mm) exposed sections of the wires bonded 3–5 mm apart near the center of one side of a 2–3 cm² rectangle of dacron-reinforced Silastic sheet. The Silastic “patch” was shaped individually for each recording site to allow firm anchoring by suturing to muscle fascia, holding the exposed wires against the surface of the muscle and insulating them from signals originating in overlying muscles. Variations in “patch” design included a double adjacent patch – with two pairs of wires – for placement over the anterior SOL-PLT border, and a double sided patch – with a pair of exposed wires on each side – for placement between TA and EDL. Figures 1D and E provide schematic information about the design and configuration of the implanted recording devices.

Cross-talk among EMG signals was a particular concern in the design and implantation of recording electrodes. In our experience, such crosstalk is usually seen as a temporal correlation between signals recorded in one muscle and those recorded in an adjacent muscle. In pilot experiments, patch electrodes with the designs and placements reported here were completely effective in removing such correlations where they were known to be a problem (e.g. FDL and FHL, see O'Donovan et al. 1982). Because of the large numbers of simultaneously implanted muscles, all from the same anatomical compartments of the shin and calf, we were always able to compare the EMG records of any given muscle with those of all potential sources of crosstalk, making certain that questionable patterns of correlation had not occurred. Furthermore, many of the muscles, including most of the small muscles for which crosstalk might be expected to be a problem, were instrumented with strain gauges in at least one preparation, making it possible to confirm that the EMG patterns which we report as typical were, in fact, associated with active force generation.

Tendon force transducers

In five animals, tendon force transducers were implanted as described in detail elsewhere (Walmsley et al. 1978; Loeb et al. 1980; O'Donovan et al. 1982) to provide continuous records of individual muscle force output. Balanced two arm sensors (BLH-SR-4) were used; the exact mechanical design of these transducers was governed by available space in the leg and length of exposed tendon (see Fig. 1D and E). In no case were more than two force transducers implanted in one animal. Force records were obtained from the FDL tendon of two animals, using devices and placement similar to that of O'Donovan et al. (1982). The long TP tendon adjacent to that of FDL is also very suitable for such recording; in three animals force records were obtained from TP. Although the PLT tendon proximal to the calcaneus is too short for this style of force transducer, a large portion of the tendon passes over the calcaneus and becomes the tendon of origin for the FDB. This unusual series arrangement of muscles for digit flexion was examined in three animals with force transducers placed on the broad tendinous sheet which provides the origin for FDB. The stainless steel baseplate for these transducers was specifically designed for this tight compartment and uniquely shaped tendon. In one animal a force transducer was placed on a complete achilles tendon, providing a record of the major ankle plantar-flexion forces. The active elements of the force transducers were attached to Teflon-insulated wire leads (see above), and the entire device was coated with Parylene-C. Whenever possible, fascia was sutured around the implanted device to secure it; however, the design of the steel fingers which encircled the tendon was probably the primary factor in preventing dislodgement of the device.

Muscle length gauges

Length gauges made of Silastic tubing filled with hypertonic saline (described in detail by Loeb et al. 1980) were implanted and calibrated to provide records either of actual muscle length changes or of joint angle changes. Muscle length records were obtained for the gastrocnemius (all six animals), PLT (three animals), FDL (two animals), and TP (two animals). Gauges for MG/LG were sutured proximally to ligamentous tissue or to a small screw near the muscle origin above the knee, and distally either to the calcaneus (using a small hole drilled transversely through the bone) or to the MG tendon. The latter type of distal attachment was also used for PLT length gauges, which were sutured to the PLT tendon after it had been partially dissected free

of the achilles tendon bundle. Gauges for measuring FDL or TP length were sutured proximally to the tibia (using a small hole drilled through the tibial crest about 40 mm below the knee) and were sutured distally to the appropriate tendon. When force transducers were also placed on these tendons, the length gauges were attached distal to the force gauge so that the small amount of force generated by the elasticity of the Silastic tubing would not contribute to the force records (see Fig. 1D and E).

Joint angles

In order to interpret muscle length changes in relation to limb kinematics (an issue of particular importance for multi-joint muscles) length gauges were also used to obtain records of knee and ankle joint angles. For the knee, in two animals a gauge was fastened proximally to a stainless steel screw affixed to the medial surface of the femur, about 30 mm above the knee. The distal end was sutured to a small hole drilled in the tibial crest (see above). This type of knee angle gauge passed medial to the distal limb musculature (e.g. triceps surae), minimizing distortion by bulging muscles. In three animals length gauges were attached across the ankle joint, sutured to previously described holes in the tibia and calcaneus.

The gauges used for the knee and for the MG/LG and PLT were constructed from larger tubing stock (Sil-Med SM1150 0.045" i.d. x 0.065" o.d.) and ranged in length from 40–55 mm. The gauges used for the ankle and the smaller muscles were correspondingly smaller (Dow-Corning 602-135 0.020" i.d. x 0.037" o.d.) and ranged in length from 25–35 mm. The electrical leads for both sizes of gauges were Teflon-coated, multi-stranded stainless steel wire (see above).

Connector

The wire leads from the implanted devices were gathered in two or three bundles and led subcutaneously to the lower back, where they exited through the skin. A single lead with an exposed wire loop at the end was anchored subcutaneously in the lateral thigh to serve as a common ground electrode. The wires were individually soldered to contacts of a small printed circuit board on which was mounted a multi-pin connector. The board was fixed to a Dacron reinforced Silastic "saddle". This "saddle connector" was then fastened to the back of the cat over the wire exit points using four heavy synthetic sutures through the skin and lumbosacral fascia. In closing all of the surgical wounds, care was taken to restore as many fascial planes as possible, to insure minimal modification of structure and function within the limb.

Data collection

Data collection was accomplished by recording signals from the implanted devices on FM tape (up to 18 channels) while videotaping the movement (two-camera/split screen arrangement using Telemation plumbicon cameras and a Sony VO-2800 cassette recorder). Electrical signals were led via a helical ribbon cable from the cat through amplifying and signal conditioning devices to the tape recorder. EMG signals were differentially amplified and filtered (50–2000 Hz bandpass). Each force transducer was connected as two arms of a DC bridge circuit (100 Hz bandpass); each length gauge was connected to an AC bridge circuit with a rectified and integrated output (20–30 kHz carrier, DC–100 Hz demodulated output). For synchronization, a digital time code generator (Datum 9300) provided a millisecond clock on the video picture and an IRIG-B code signal on one channel of the tape recorder.

Treadmill speed was recorded continuously (when used) on one tape channel, multiplexed with a code for stimulation events.

To assist in obtaining kinematic information from video records, skeletal landmarks were carefully palpated and marked on the overlying skin with contrasting. Marks were placed over the metatarsal/phalangeal joint (lateral aspect), ankle (lateral malleolus), hip (femoral greater trochanter), iliac crest, and ischial tuberosity.

Data collection took place on one or two consecutive days after the animal was judged to have completely recovered from the surgery (ten to twenty eight days post-operatively). The testing protocol would begin with jumps and drops. Each animal had been trained to leap onto and off of a counter for a food reward; the height of the leaps varied from 0.45–1.0 m. Animals were dropped in an upright position from a height of about 0.75 m. Then the animal was placed in an enclosure on a treadmill (about 1.3 m long and 0.3 m wide) for walking and running. All animals walked steadily at speeds of 0.6–1.0 m/s for five to ten minutes; running at higher speeds (e.g. 1.5 m/s) could be maintained for only fifteen to thirty seconds. Finally reflex scratching and paw shaking responses were elicited. Paw shaking was triggered by the presence of adhesive tape on the plantar pad while the animal walked on the treadmill (Smith et al. 1980). Each tape application would typically elicit shakes for three-six steps before the tape fell off or the animal habituated. Scratching was triggered by light cutaneous stimulation of the ipsilateral pinna; scratches varied in form and intensity, including waving the paw in the air, scratching the ipsilateral shoulder, and scratching the ear vigorously.

Terminal experiments

Calibration experiments were conducted immediately after data collection, under deep pentobarbital anesthesia. First, a complete range of individual and combined joint angles was passively produced and calibration records (using an electrogoniometer) were taped along with the implanted transducer signals for analysis of joint angle and muscle length records. Then the length and force transducers were calibrated *in situ*. With the limb immobilized by pins and clamps, the distal end of the tendon was detached and fixed to a cable and hook passing over a pulley so that the majority of the tendon remained in place along its original axis. Calibrating weights were then hung on the hook and records made of the analog force signal. At the same time, increases in muscle length were measured and recorded for comparison with length gauge signals. Finally, after the animal was sacrificed, careful measurements were made of limb segment lengths and relative device positioning. In addition, all implanted devices and electrodes were inspected for possible post-surgical shifts in location. Force gauges were removed for possible reuse; no other devices were reused.

Data analysis

Videotape and analog records were inspected jointly to identify both typical and unusual behaviors. Permanent records of selected sections of the analog data were then made using a 10-channel oscillographic recorder (Honeywell, 1858 CRT Visicorder). The recorded time code was used to match the analog signals with the video picture (viewed field-by-field using a Sony video disc, 16 ms temporal field resolution). Significant events such as foot contact, reversals in joint movement, and movements of non-instrumented body parts were identified and marked on the oscillographic records. Then similar movements were grouped together and examined for consistent patterns. Analysis of the reflex responses to stimulation of cutaneous nerves is reported separately (Abraham et al. 1985).

KEY TO FIGURE ABBREVIATIONS AND CALIBRATIONS

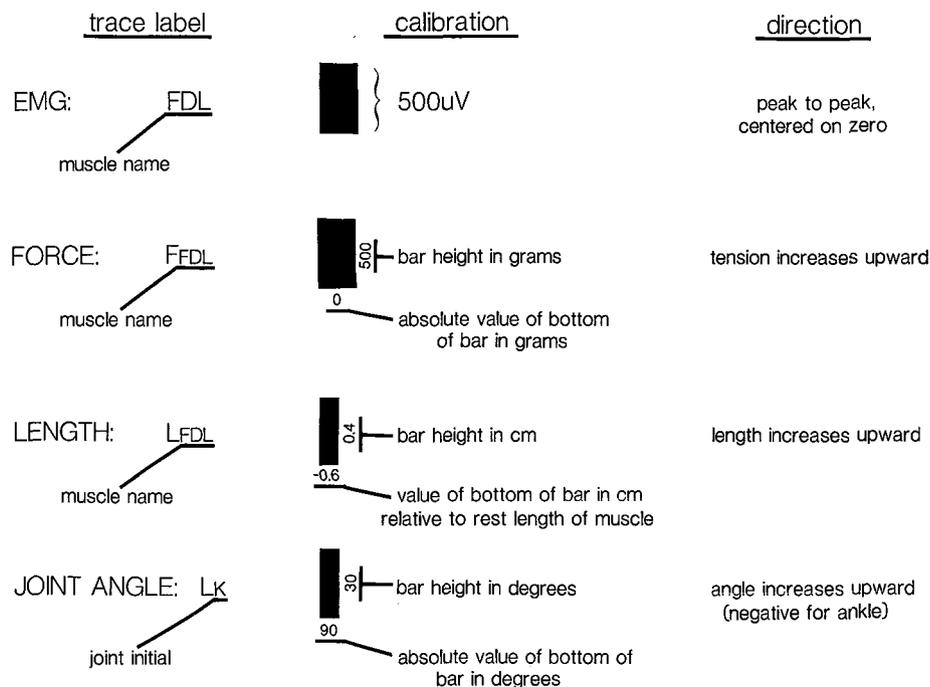


Fig. 2. Key to labels and calibrations in Figs. 3-9

Results and interpretation

The results are organized by activity; each is accompanied by representative examples of raw data and a brief discussion of significant points. Figure 2 contains a key for interpreting the sample records in Figs. 3-9. We have used the terms "flexor" and "extensor" to refer to anatomical action at the ankle joint, using descriptors such as "stance phase" and "swing phase" to refer to functional synergies of recruitment.

Standing

The role of the cat distal hindlimb muscles during standing is to stabilize joints against gravitational forces. At the knee, ankle, and metatarsal-phalangeal joints the primary axes of rotation are transverse; hence the flexion and extension components of muscular force are of most interest. Because of the non-vertical alignment of the bones in the leg and the orientation of major muscular lines of force, stable anteroposterior posture can be maintained (at least theoretically) by balancing the respective gravitational moments with single muscular moments at

each joint. Minor adjustments can likewise be made by modulating the output of single muscle groups (with respect to the opposing gravitational force), rather than by recruiting activity in an antagonistic muscle or muscle group. Lateral stability, on the other hand, requires either simultaneous or rapidly alternating activity in antagonist muscle groups because the gravitational force vectors fall close to or through the joint centers.

From one animal we recorded patterns of postural EMG activity during standing with each foot on a separate load cell. In this way we were able to examine the contributions of individual muscles to the diagonal postural patterns associated with reflex leg lifting in response to foot taps as described by Coulmance et al. (1979). Figure 3 shows the activity of left hindlimb muscles during independent lifting of each leg. The diagonal pattern (reduced load bearing in the leg diagonally opposite the lifted leg) is clearly evident in the force records; i.e. the left hindleg shows increased weight bearing when the right hind- or left forelegs are lifted, and reduced weight bearing when the left hind- or right forelegs are lifted.

The SOL muscle, which is one of the most active during quiet standing, clearly showed the greatest extent of participation in these postural adjustments.

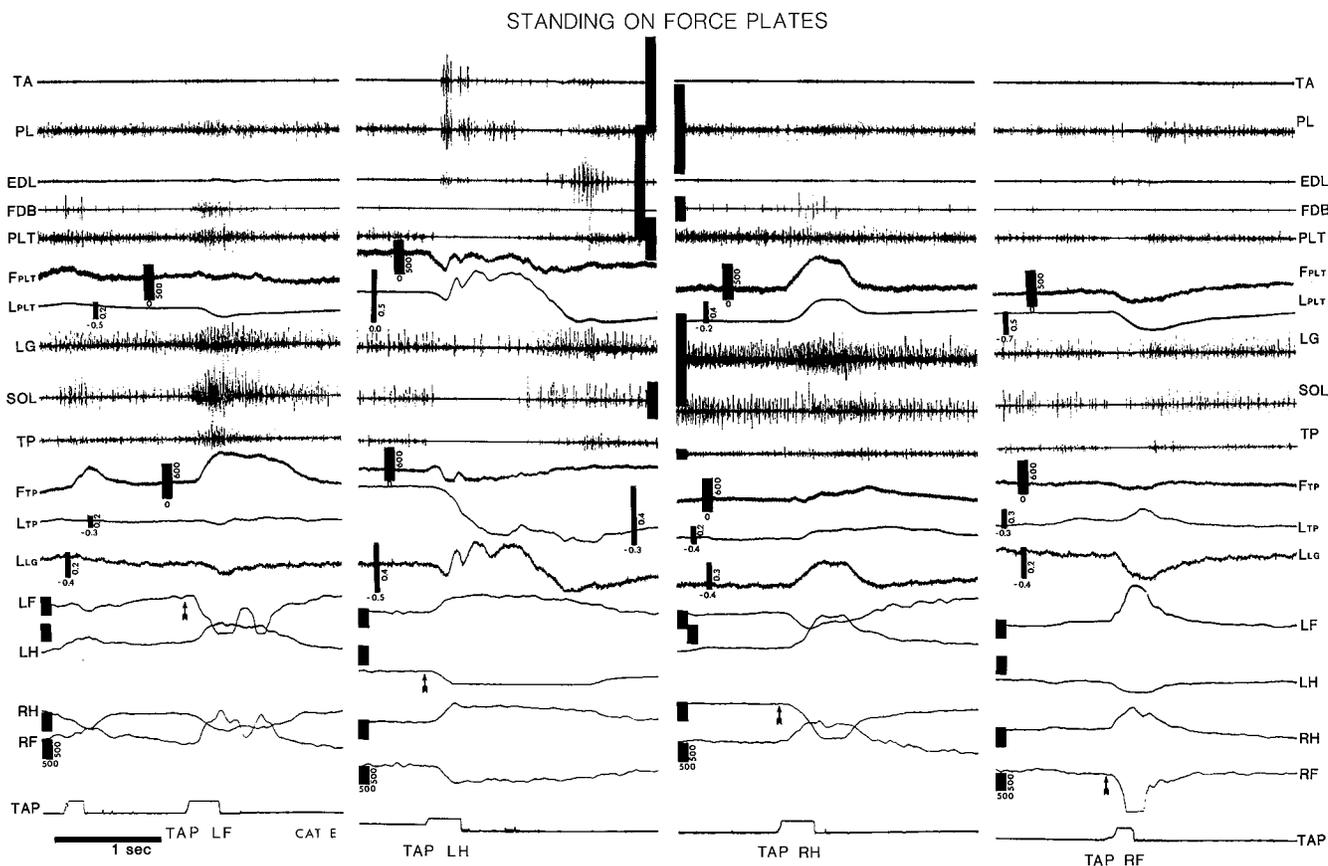


Fig. 3. Left hindlimb responses to cutaneous-tap-elicited reflexive footlifts. The bottom five traces indicate weight borne by each leg (in grams) and the contact of the tapping stylus; other traces are EMG, force, and length records from indicated muscles. Arrows indicate the onset of each reflex-eliciting tap, which is followed by complete lift of this foot indicated by weight going to zero

Increased weight bearing was accompanied by increased activity; decreased weight bearing (limb yielding) was accompanied by a silent period in SOL. Other apparent extensors with similar patterns included TP, PLT and, to some extent, FDB and LG. The increase in PL activity with increased weight bearing probably related more to lateral ankle stabilization as there was no other indication of ankle dorsiflexion activity (e.g. TA or EDL EMG activity).

Walk

The kinematics of the cat hindlimb during locomotion have been described in detail previously (Goslow et al. 1973; Forssberg et al. 1980; Wetzel et al. 1975; Wetzel et al. 1976). Throughout this paper, the step cycle phases identified by Phillipson (1905) are used (see Table at end). The role of the distal hindlimb musculature during walking is a variation of that described for standing. During the stance phases (E_{2-3}), the active muscles (most of the ankle and knee

extensors) are stabilizing the limb dynamically, maintaining the height of the hip while distal joints change angle so that the hip moves forward over the foot. In the E_2 phase of stance these extensor muscles are working while lengthening (yielding), while during E_3 the limb is extending and so the extensor muscles are shortening while resisting gravity. Lateral stabilization appeared to be very similar to that of standing. During the F portion of swing, the active muscles (including most of the ankle dorsiflexors) actively shorten to propel the foot upward and forward. This action meets little resistance (almost entirely the inertial mass of the limb itself). During the E_1 phase of swing, ankle and knee extensor muscles shorten as the limb extends so that the foot strikes the ground in front of the hip. This contraction is initially unloaded, using momentum generated in F, and includes a variable amount of preactivation of the ankle and knee extensors prior to footstrike. Figure 4 contains records from several experiments showing normal walking patterns. The general EMG patterns of ankle extensor muscles (rising rapidly during E_2

WALKING ON TREADMILL

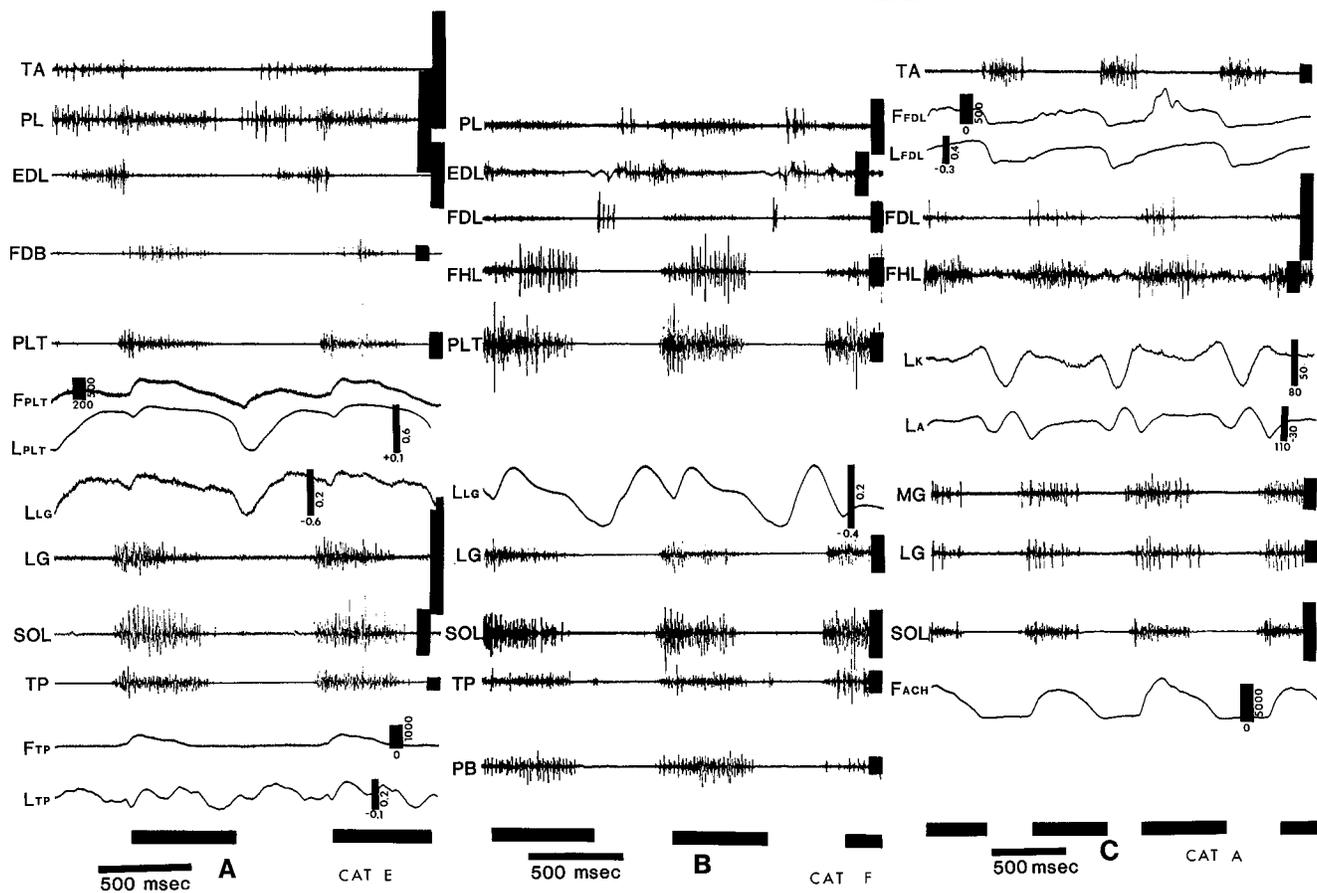


Fig. 4A-C. Selected records of left hindlimb patterns in normal walking. Traces show EMG, force, and length of indicated muscles, and joint angles. Horizontal bars at bottom indicate stance phase of walk

and tapering off during E_3) and ankle flexor muscles (bursting quickly in F) were consistent with previous reports (Engberg and Lundberg 1969; Tokuriki 1973a). However the inclusion of length and force gauge records revealed several interesting details (see Fig. 4).

TP (which was found in an acute stimulation preparation to contribute to ankle extension as well as inversion) appeared to be modulated somewhat differently than other ankle extensors. TP EMG activity remained high well into E_3 , unlike SOL, LG, or PLT (Fig. 4A and B). TP force records confirmed the active contribution of this late activity to the movement, while TP length records suggested that this action was to a large extent isometric (note magnified scale in Fig. 4A); early stance force increments were due in large part to active muscle lengthening. Interestingly, the anatomy of the TP insertion just distal to the center of rotation of the ankle joint is such that it generates more extension (rather than primarily inversion) force when the

ankle is already in an extended position such as found during the end stance push-off. Earlier in stance, its ankle inverting action probably dominates and appears to be countered by both peroneal muscles (PL and PB).

Comparison between the PLT and triceps surae is also interesting because, although both contribute to ankle extension, the PLT tendon extends beyond the calcaneus to form the origin of FDB and thus PLT influences digit action. Length gauge records showed that while LG was shortening throughout E_3 , PLT was remaining more nearly isometric (cf. Fig. 4A). This was caused by passive dorsiflexion of the digits as the foot rotated forward over the plantar pads.

The EMG records of PL showed evidence of activity during both the swing and stance phases of walking (Fig. 4A and B). The F phase activity is consistent with the anatomical characterization of PL as an ankle dorsiflexor, while the E_1 , E_2 activity must reflect lateral action (everting or stabilizing against inversion).

TROTGING ON TREADMILL

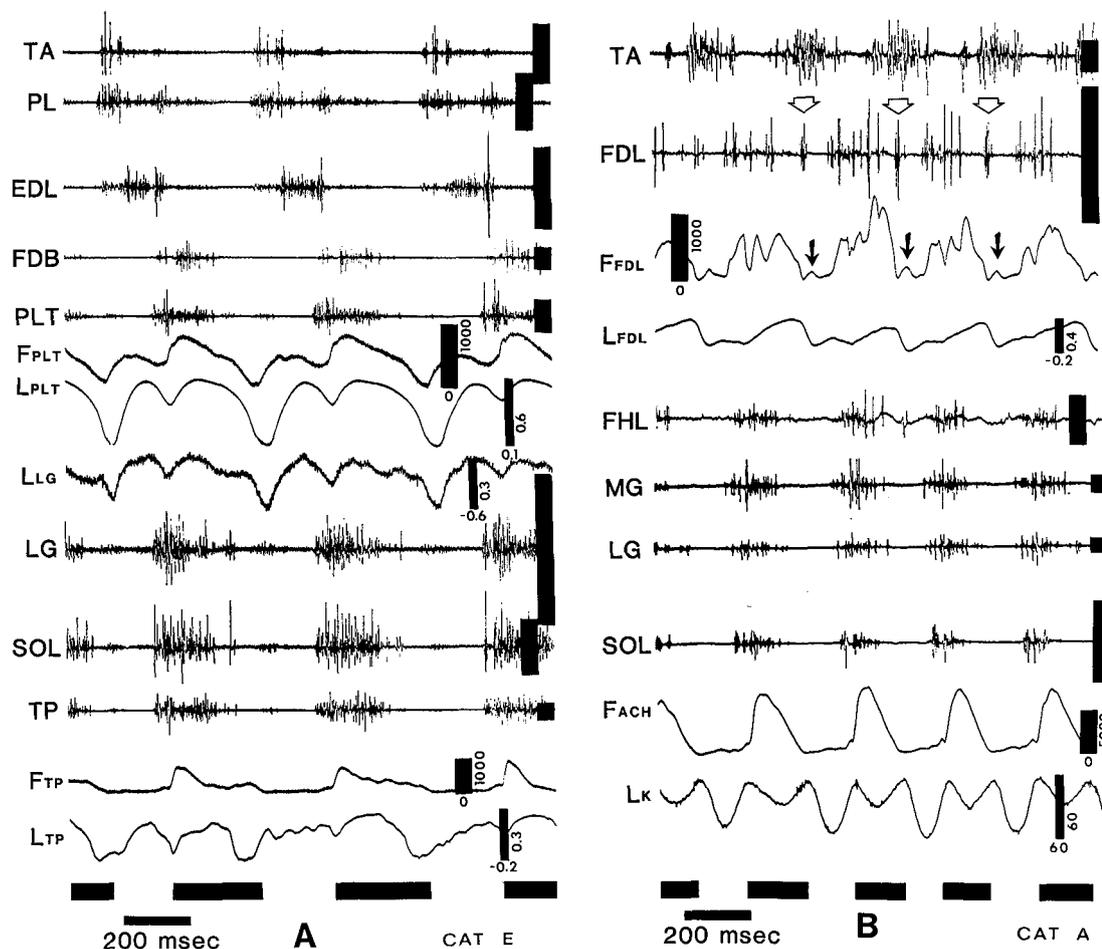


Fig. 5A and B. Selected records of left hindlimb patterns in normal trotting. Traces show EMG, force, and length of indicated muscles, and joint angles. Horizontal bars at bottom indicate stance phase of walk. In B note the sensitivity of the FDL force gauge to EMG bursts during muscle lengthening. Open arrows indicate bursts during shortening; solid arrows indicate associated force peaks

Trot

Each of the implanted animals would maintain a trotting gait for at least 20–60 s. Figure 5 contains data from two such episodes. Mechanically, the major differences between locomotor speeds for individual muscles are duration and level of activation. Nearly every muscle was more active (based on EMG and/or force records) during trotting than walking (though not in exact proportion); phase relationships were very stable. Increased EMG activity led to large increments in force output during isometric or loaded conditions (E_2), and rapid increments in muscle length during shortening or unloaded conditions (F, E_1). The greatest increases in EMG amplitude occurred during the unloaded phases (see Fig. 4A and Fig. 5A), where inertial

loads presumably predominate (e.g. TA, FDL in F; LG, EDL in E_1).

Examination of the PLT and LG length gauges during trotting revealed another important aspect of difference. The gastrocnemius appeared to function as a typical two-joint muscle, minimizing energy expenditure during locomotion by maintaining a relatively constant length (Elftman 1966; Armstrong et al. 1977; see also Walmsley et al. 1978). Thus knee and ankle action combined to reduce length changes, allowing the gastrocnemius to become an efficient, stiffer spring for storage and release of mechanical energy. PLT, however, continued to undergo large length changes, particularly during early stance, because of the passive dorsiflexion of the digits. The force exerted against this dorsiflexion was distributed in time between PLT and FDB. Thus at the middle of

JUMPING UP

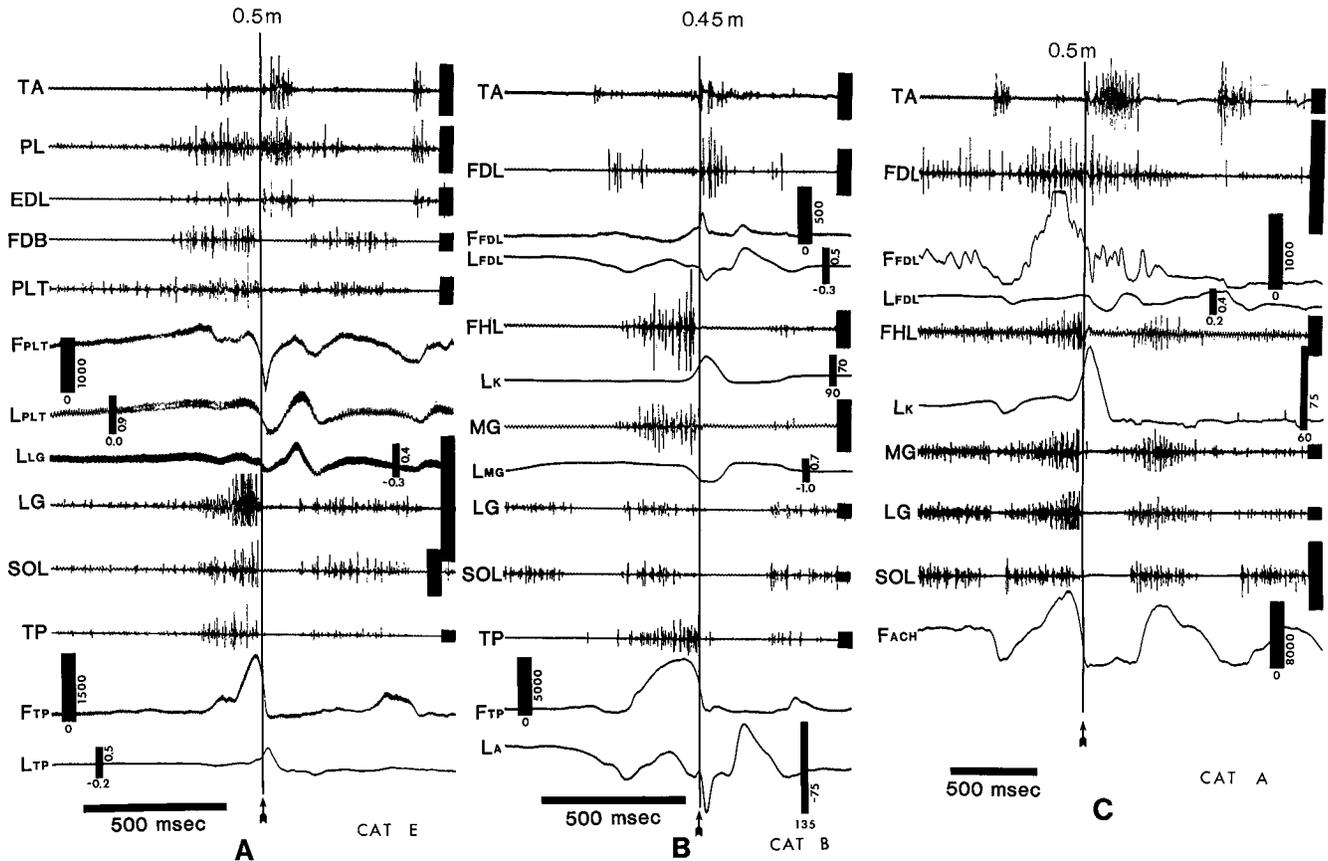


Fig. 6A-C. Selected records of left hindlimb patterns in jumping up to a platform, three different cats. Traces show EMG, force, and length of indicated muscles, and joint angles. Arrows and vertical lines indicate time of foot leaving the ground. Height of each jump is indicated at top

this extensive active lengthening, PLT activity diminished while FDB activity increased. At this same time the onset of ankle plantarflexion was beginning to reduce the effectiveness of PLT as a digit flexor. Also, it is likely that the pulley around the calcaneus had reached the anatomical stop which prevents transfer of tension to the distal part of the PLT/FDB combination after about 5 mm motion (Goslow et al. 1972). Thus, the tension recorded here for PLT by a strain gauge distal to the calcaneus was probably coming primarily from the active lengthening of the much weaker FDB.

The bursting activity of FDL in both the walk and the run was complex and irregular. The most consistent feature was a brief burst of EMG just at the beginning of F, shown by arrows in Fig. 5B. This occurred during the rapid plantarflexion of the toes as the foot was unloaded, but the active tension in FDL resulting from this EMG activity would be

expected to be delayed by about 50 ms. The shortening was thus completed primarily by the high degree of passive elasticity which has been noted in this muscle previously (O'Donovan et al. 1982). The active tension peaks (solid arrows) corresponding to the end-stance EMG (open arrows) can be seen near the length minima. The lengthening which follows is presumably the effect of the ankle dorsiflexion initiated by TA and other dorsiflexors which turn on just before the end of stance. Thus the biarticular FDL completes the digit flexion as a stiffly elastic strut which transfers momentum from the dorsiflexing foot to the plantarflexing toes. The activity of FDL during stance occurred in irregular bursts and was seen only rarely during slower locomotion (see Fig. 4B and C). In contrast, FHL was consistently recruited with other ankle extensors during stance and never during flexion, despite its similar anatomical action to FDL and in agreement with previous reports (O'Donovan et al. 1982)

Jump

The jump analyzed here was a ballistic action involving complete leg extension to propel the body upward against gravity. This action was undertaken with a pattern of sequential activation (proximal to distal) of muscles ending with the digit plantar flexors. All ankle extensor muscles actively shortened to contribute to this action (Fig. 6). The brief duration and high intensity of these contractions led to force output exceeding that found in normal locomotion. After takeoff and during flight the hindlimbs were brought forward in a flexed position in preparation for landing on the target surface. This was accomplished by active shortening of the unloaded ankle flexor muscles (TA, EDL) and FDL, again used as the principle toe flexor. Landing involved primarily an active lengthening on the part of the limb extensors, with some additional stabilizing activity which was specific to each performance.

Figure 6 displays data from jumps which were performed up to a surface about 0.5 m above the starting platform. The ankle extensor functions of SOL, MG, LG, PLT, FDB, FHL and PB were clearly revealed in the EMG activity buildup which ceased abruptly as the limb was unloaded at takeoff. The general limb flexion activity during flight can be seen to be against low resistance (e.g., FDL force records in Fig. 6B and C). The alternating activation of the anatomical synergists FDL and FHL seen here is consistent with a previous report (O'Donovan et al. 1982); the flight FDL activity was clearly shortening (flexing the digits) against low load, despite the rapid dorsiflexion of the ankle, which would tend to stretch this muscle. The cocontraction of EDL and FDL during flight may be related to EDL's ankle dorsiflexion action and/or stabilization of the phalanges to permit claw protrusion by FDL. The forceful cocontraction of FDL and FHL during extension (seen in Fig. 6C only – not in B) is typical of maximal digit flexion efforts when muscle shortening and (possibly) active claw protrusion actually occurs.

Drop

Landing from a fall generates rapid lengthening of ankle extensors, which must be preactivated to provide adequate stiffness against gravitational force and body momentum; high forces should be seen in all ankle extensor muscles. Figure 7 contains data from one such drop. The regularity and synchronization of EMG among the three triceps muscles is striking during the freefall and disappears during

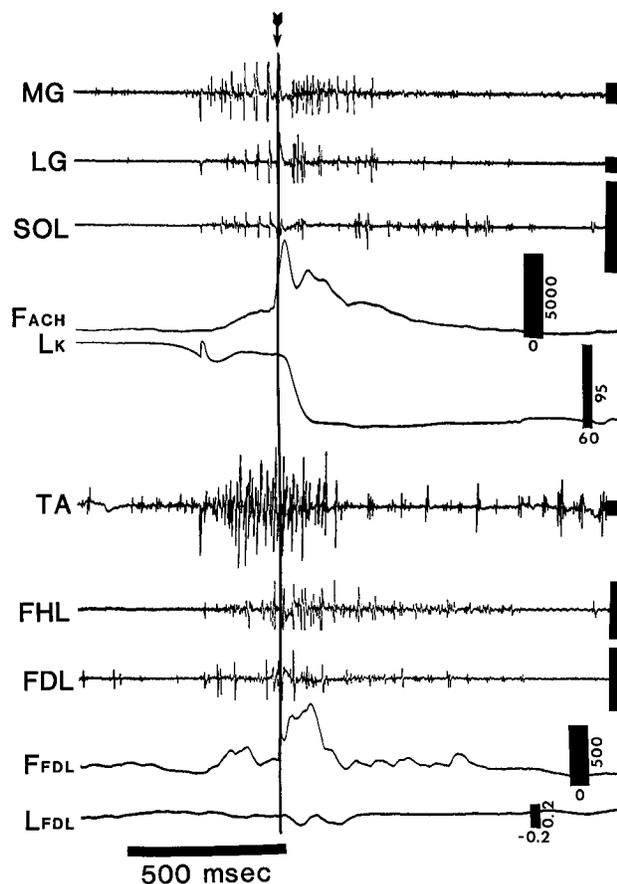


Fig. 7. Sample pattern of the left hindlimb during landing from a drop (about 0.75 m) on a tile floor. Traces show EMG, force, and length of indicated muscles, and knee angle. Arrow and vertical line indicate time of foot contact with the ground

load bearing. The general coactivation of FDL and FHL along with more clear cut extensors and flexors (see TA) shows that these muscles can indeed act together in certain circumstances and may relate to the "facultative" activity described by O'Donovan et al. (1982). Here the goal seems to be a high degree of stiffness to absorb the sudden load on landing. However, the detailed timings of FDL and FHL EMG bursts are different from each other and from the tightly synergistic triceps surae (MG, LG, and SOL), suggesting different sources of command signals.

Shake

The paw shake analyzed here appeared to be a very functional attempt to remove tape from the plantar surface of the foot (see Methods and Smith et al. 1980). The limb was drawn forward (flexed) and then rapidly extended backward, with a forceful reversal

PAW SHAKING DURING WALK

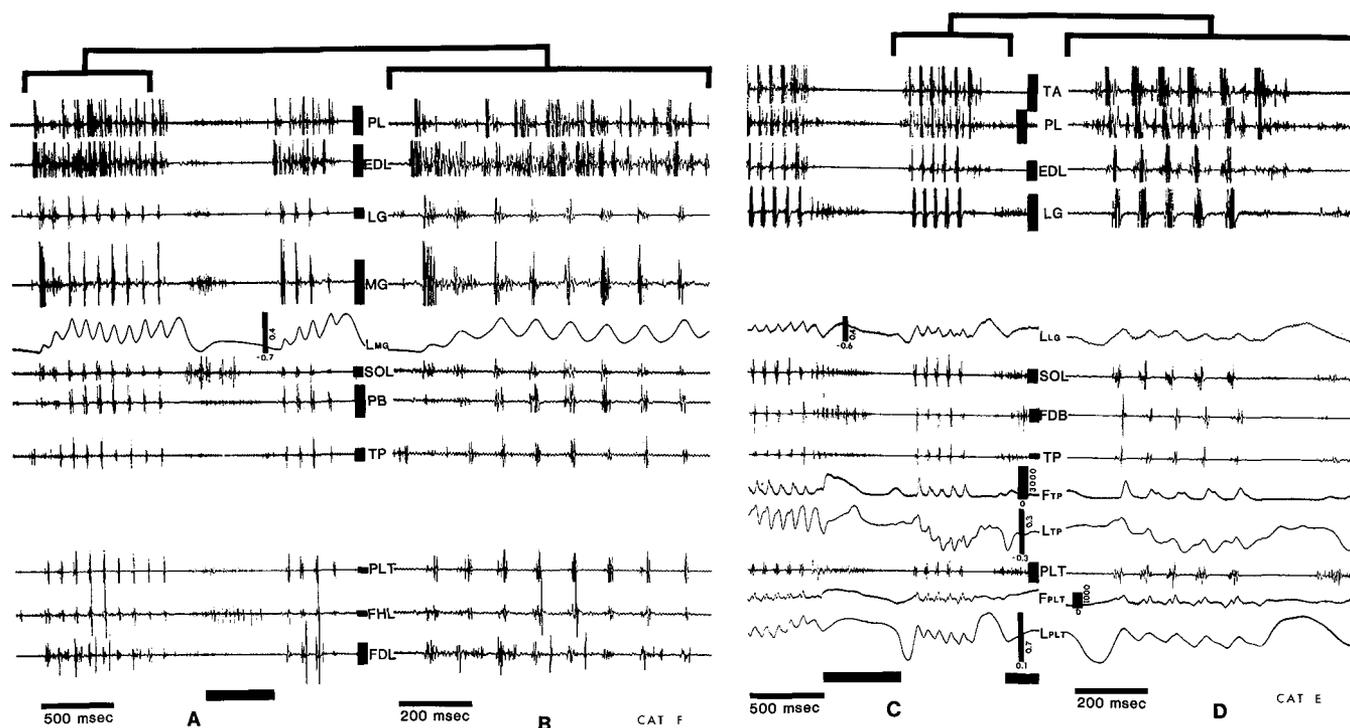


Fig. 8A-D. Two examples of left hindlimb patterns during paw shakes elicited while walking on the treadmill. Traces show EMG, force, and length of indicated muscles. In A and C horizontal bars at the bottom show stance phase of locomotion (between shakes); B and D are expanded sections of A and C as shown at top

of the backward extension in a whip-like snap. This asymmetric activity was repeated several times during a step, usually ending in a high rapid step forward. The action of the ankle flexor muscles was both to prepare for the rapid extension (a moderate, low load, shortening action) and to halt the rapid extension (an intense, high load, lengthening action). After the first flexion in a sequence, the braking action was continuous with the following flexion. The action of the ankle extensor muscles was to extend the joint as rapidly as possible (an intense, low load, shortening action). Unlike the actions of walking, trotting, and jumping, shaking involved sequential joint actions separated in time such that the knee and the metatarsal/phalangeal joints were often 180° out of phase (again characteristic of a whipping action). Figure 8 contains data displaying this sequence.

While the records appear highly synchronized, there is distinct ordering of EMG onset in each cycle of the movement. For most shakes, the sequence of muscle activation was (1) TA, (2) PL, (3) EDL, (4) LG, MG, (5) SOL, PB, (6) TP, PLT, (7) FHL, FDL, FDB. This followed a consistent flexor-extensor and proximal-distal pattern. The EMG data from the step between the shakes in Fig. 8A and C provide an indication of the high amplitude of the bursts of

shake activity, many of which saturated the recording amplifiers. The relatively low SOL activity is consistent with the report of Smith et al. (1981) that the slow twitch fibers of SOL cannot contribute to this fast activity and so are programmed to undergo more passive length changes than the other triceps muscles (Whiting et al. 1982). The high amplitude records of most other muscles were characteristic of rapid ballistic shortening activity which presumably must involve a large percentage of available fast-twitch fibers.

Scratch

Scratching was the most variable of the activities studied, with the animals exhibiting individual styles of limb and claw posture. There appeared to be a continuum of intensity which ranged from mild waving of the limb in the direction of the ear being stimulated to a vigorous, rhythmic clawing of the ear. The duration of each scratch episode was also extremely variable. In general, more vigorous and extensive scratching was elicited by more intense stimulation. As described previously by several authors (Deliagina et al. 1981; Deliagina and Feld-

SCRATCHING

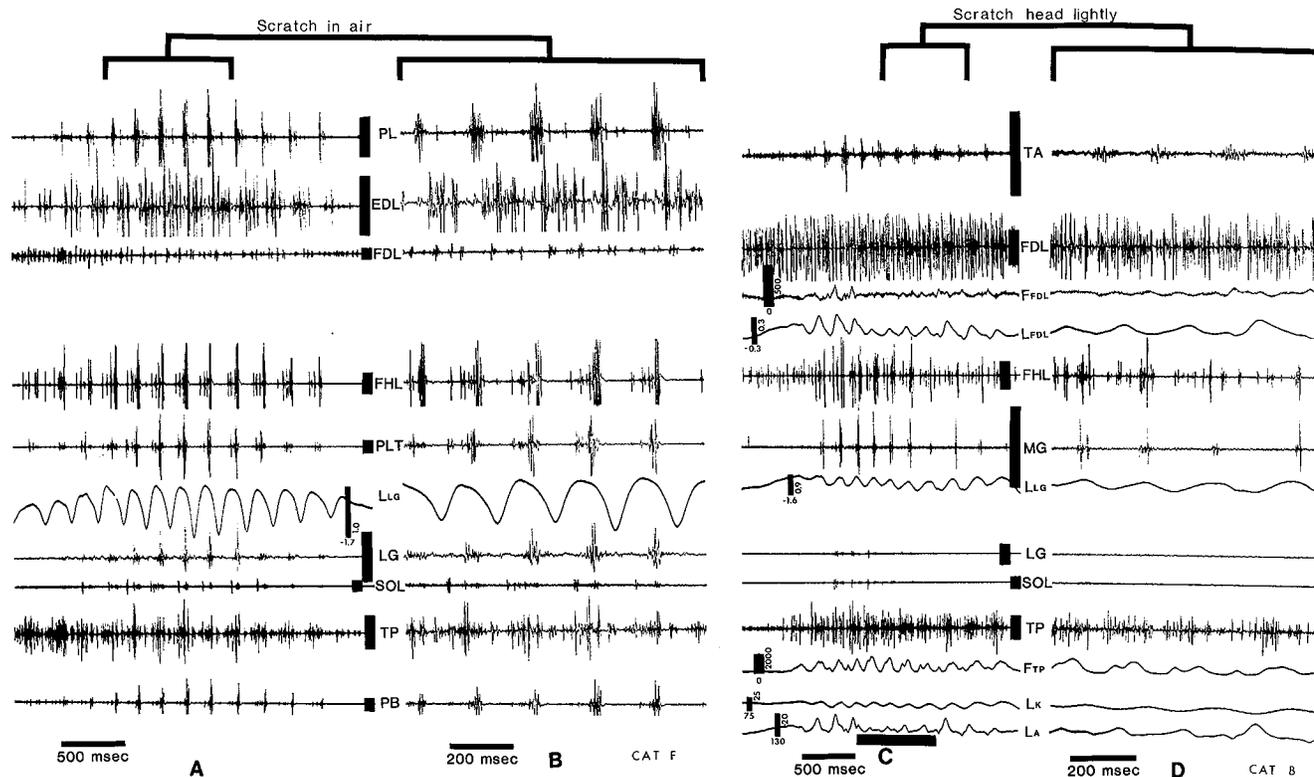


Fig. 9A-D. Two examples of left hindlimb patterns during scratching elicited by cutaneous stimulation in the ear. Traces show EMG, force, and length of indicated muscles, and joint angles. Records A and C show complete scratching segments; B and D are expanded sections of A and C as shown at top. The horizontal bar at the bottom of C indicates the time of paw contact with the head

man 1981; O'Donovan et al. 1982) scratching was composed of an initial posturing of the limb followed by a rhythmical alternation of flexion and extension at the knee and ankle. The posturing was primarily a flexion at the hip, often accompanied by medial hip rotation and/or ankle inversion, and tonic claw protrusion. The subsequent movement pattern consisted of a brief ankle dorsiflexion (moderate, unloaded shortening of the flexors) followed by a more prolonged extension (shortening of extensors); the load depended on whether the claws were contacting the body surface. When present, knee action was in phase with the ankle. The animals we studied varied in the postural orientation of the limb and in the joints involved in the rhythmical activity. These variations were due in part to the position of the animal and also to individual "styles" of scratching. Efforts were made to standardize the initial position of the animal to quiet standing; however, occasionally good scratching could only be obtained from an animal lying partially on its right side. Figure 9 contains records from two different scratching performances.

Muscles contributing to the initial posturing were PB, FHL, PLT, TP, and then PL. These muscles, as well as triceps surae and FDL, were then active during the extension phase of the rhythmical scratching, although the long lever ankle extensors (SOL, MG, and LG) were notably less active than muscles with more complex actions (e.g. TP, PLT, and FHL). Muscles acting to recover the foot in the flexion phase were TA, EDL, and sometimes PLT. As in the shake and jump, active shortening against load was produced by digit plantarflexors FHL and FDL acting together (Fig. 9C and D). The amplitude of FDL EMG records obtained during scratching exceeded those of any other behavior, perhaps because of the vigorous shortening with protruded claws. This pattern seemed to be particularly firmly associated with contact scratching by ankle extension/dorsiflexion. Non-contact scratching movements (Fig. 9A and B) showed more reciprocal recruitment of FDL/FHL. Occasionally, scratching motion was generated primarily at the hip or knee, which involved alternation by more proximal muscles and cocontraction/stabilization by the distal musculature

and skeletal segments. The large TP force records produced in scratching were caused by phasic activity superimposed on tonic ankle inversion.

General conclusions

The simultaneous monitoring of muscle activity (EMG), length, and force during a variety of normal behaviors clearly enhances understanding of the contribution of specific muscles to each activity. It also provides an internal check for possible errors and artefacts such as EMG crosstalk. In a mechanical structure as relatively simple as the cat distal hindlimb, this process provides clear support for the identification of general patterns of synergy among muscles, yet there are also instances of reorganization or regrouping of these muscles for specific tasks. In most cases those instances can be described on the basis of the mechanical properties of the muscles involved in conjunction with the length changes imposed by the trajectory of the limb motion. It appears that at least several parallel neural control mechanisms have been provided to obtain optimal mechanical results from the available peripheral elements.

An additional benefit of the recording techniques used in these experiments is the information gained about the mechanical characteristics of individual muscles during normal behavior. The relationships between muscle activation level, tension, length, and velocity have proven to be extremely complex (Bouisset 1973; Partridge 1979; Perry and Bekey 1981). Nevertheless, it is precisely this information that is needed to study motor control processes further and to understand anatomical specializations such as muscle fiber architecture and fiber type distributions. Thus it seems imperative that more attention be given to the mechanical correlates and consequences of normal patterns of motor activity, with special attention to the effects of muscle fiber types, internal muscle architecture, and the highly specialized arrangements of tendons found in most mammals.

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Abbreviations

Muscles:		Primary locomotory action:
EDL	extensor digitorum longus	dorsiflex digits
FDB	flexor digitorum brevis	plantarflex digits
FDL	flexor digitorum longus	plantarflex digits

FHL	flexor hallucis longus	plantarflex digits
LG	lateral gastrocnemius	extend ankle
MG	medial gastrocnemius	extend ankle
PB	peroneus brevis	extend ankle
PL	peroneus longus	dorsiflex ankle
PLT	plantaris	extend ankle/digits
SOL	soleus	extend ankle
TA	tibialis anterior	dorsiflex ankle
TP	tibialis posterior	extend ankle

Limbs:

A	ankle
K	knee
LF	left forelimb
LH	left hindlimb
RF	right forelimb
RH	right hindlimb

Step cycle phases:

E ₁	first extension, late swing phase prior to footfall
E ₂	second extension, early stance phase
E ₃	third extension, late stance phase
F	flexion, early swing phase

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