

## REFLEXES IN CAT ANKLE MUSCLES AFTER LANDING FROM FALLS

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*(Received 9 February 1977)*

### SUMMARY

1. Electrical activity and length of ankle muscles were recorded by telemetry during free fall and landing in cats.

2. After foot contact, there was a delay in onset of stretch of ankle extensors of between 8 and 11 ms. High-speed cinematography showed the delay to be associated with rapid initial dorsiflexion of the toes.

3. Electromyograms (e.m.g.) from lateral gastrocnemius increased in amplitude prior to landing. An early depression of lateral gastrocnemius e.m.g. commenced at 8 ms after foot contact, and was followed by a large peak of activity commencing some 8 ms after the first increase in lateral gastrocnemius length.

4. Local anaesthesia of the plantar cushion did not alter this pattern of response.

5. The early inhibition of lateral gastrocnemius was attributed to the action on lateral gastrocnemius motoneurons of non-cutaneous afferents responding to the initial toe dorsiflexion. Additional autogenetic inhibition may also have contributed.

6. The subsequent peak of e.m.g. was at a latency consistent with a rapid stretch reflex, and occurred soon enough for the resulting active tension to contribute significantly to the extensor force during body deceleration.

### INTRODUCTION

In normal conscious mammals, rapid stretching of a muscle as a result of sudden imposed changes in load generally leads to reflex activity of that muscle (Hammond, 1955; Newsom Davis & Sears, 1970; Evarts & Tanji, 1974). As is the case in the forelimb muscles, the e.m.g. responses of human

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ankle extensors to sudden stretch include monosynaptic, as well as long-latency components, the latter having been designated 'functional stretch reflexes' by Melvill Jones & Watt (1971*a*).

It may seem surprising that the rapid dorsiflexion of the ankle which occurs after landing from an unexpected fall, apparently does not result in detectable reflex responses in human ankle extensors (Melvill Jones & Watt, 1971*a, b*). It has been shown that e.m.g. activity is generated in these muscles during the fall, in anticipation of the moment of landing (Greenwood & Hopkins, 1976*a*). It was argued by Melvill Jones & Watt (1971*a*) that, even if they had been present, functional stretch reflexes would have come 'far too late to contribute to the muscle deceleration of the fall'. In contrast, Greenwood & Hopkins (1976*b*) reported consistent e.m.g. stretch responses in human soleus upon landing after a downward step.

Compared to man, the metatarsals of the cat are much longer, relative to body length. After landing from falls of between 0.2 and 0.6 m, cat ankle extensors undergo a lengthening contraction for about 100 ms, during which time their spindle primary afferents are excited to very high firing rates (Prochazka, Westerman & Ziccone, 1977). In view of the relatively lower rate of ankle rotation, and the much smaller reflex latencies in the cat (e.g. monosynaptic reflex e.m.g. response *ca.* 8 ms after onset of stretch), there would seem to be abundant time for a reflex response to be functionally significant (assuming a delay of *ca.* 50 ms between e.m.g. and the peak of the resulting force).

Indeed, the e.m.g. of gastrocnemius in cats falling from a height of 0.5 m has been shown previously to build up from *ca.* 200 ms before landing, to reach a peak at the time of foot contact, and then to endure with diminishing over-all amplitude for about 100 ms thereafter (Watt, 1976). In contrast to his findings in humans, it was presumed by Watt that stretch reflexes, after contact with the ground, would contribute to the late phase of muscle activation.

The present experiments further investigated this question. It will be shown that strong and rapid reflex responses occur in the ankle muscles after landing. High speed cinematography, combined with telemetry of e.m.g. and muscle length, indicated that the response in the ankle extensors included components attributable to the early dorsiflexion of the toes which preceded ankle dorsiflexion. The possibility of autogenetic inhibition contributing to this response could not be excluded.

Local anaesthesia of the footpads was used to investigate the way in which cutaneous afferent activity might influence the muscle reflexes.

## METHODS

E.m.g. electrodes were implanted in lateral gastrocnemius and tibialis anterior muscles of six cats. At the same time, length gauges were implanted between the calcaneus and the head of the tibia on the medial side of the leg (Prochazka, Westerman & Ziccone, 1976). Ultra-flexible cables from these sensors were passed subcutaneously to a head-piece, to which a small 2-channel FM-FM transmitter could be attached.

Recordings of e.m.g. from one muscle, together with the monitored length signal, were transmitted to (and received by) an FM-FM decoder during a series of drops, and stored on magnetic tape (Tandberg 100 FM). The signals were analysed subsequently using a DEC PDP-11 and a DEC PDP-8 computer.

*Implantation.* Precautions were taken to ensure the maximum possible degree of sterility. The implantation procedure was performed under Halothane anaesthesia, and lasted ca. 2 h.

An in-dwelling jugular catheter was led subcutaneously to the head-piece and terminated in a rubber-capped hub. The e.m.g. electrodes consisted of unshielded pairs of fine Polyvinylchloride-insulated multi-stranded stainless steel wires (shielded wires had previously been used, but no significant differences in noise immunity had been observed). The ends of the wires, with ca. 1 mm of insulation removed, had been inserted into the lumen of 27 s.w.g. stainless steel shafts and firmly attached by crimping. The shafts were passed through the muscle, bent over, and cut off so as to form a right-angled hook (1 mm  $\times$  1 mm), which was then pulled back under the epimysium, thus anchoring the electrode.

The mercury-in-rubber length gauges (Prochazka *et al.* 1976) were attached at the distal end by a 20 s.w.g. pin through the calcaneum and, at the proximal end, by 2 such pins at the head of the tibia. Shielded, insulated connecting cables were passed subcutaneously to the head-piece.

Wounds were sutured closed in layers, the cat was treated with penicillin, and acetylpromazine was administered to minimize discomfort during recovery. The implants were borne with no apparent distress, and an initial slight limping gradually disappeared during the first 3 d post-operatively.

*Drop trials.* The experiments were conducted from 5 to 21 d after implantation. At the beginning of a recording session, the telemetry capsule was attached to a bayonet-socket moulded into the head-piece, and appropriate electrode connections were made. In a given session, drops from 0.1, 0.2, 0.3, 0.4 and 0.5 m were studied. For each ht., muscle length and e.m.g. were recorded for 50 drops.

Prior to each drop, the cat was picked up by the experimenter, its wt. being supported under rib-cage and abdomen, and raised so that both forepaws and hind paws were roughly aligned with an appropriate point on a nearby vertical scale. The initial ht. is estimated to have varied between  $\pm 0.05$  m for any given nominal ht.

The cat was dropped as suddenly as possible, so that its left hind paw (leg carrying sensors) landed on a contact plate (0.05  $\times$  0.08 m).

*High-speed cinematography.* In order to elucidate the kinematics of free fall and landing, 5 drop trials were filmed at rates ranging from 800 to 1400 frames/s using a 'FASTAX' variable speed camera with Ilford mark V, 16 mm monochrome 400 ASA film. The camera automatically calibrated the film with 1 ms markers.

Two 2 kW spotlights were used to give a light level over the area of interest of ca.  $7.5 \times 10^4$  lm/m<sup>2</sup>, allowing an iris setting of f(3.3).

The left hind limb of the cat was shaved, and black ink was used to mark the skin over the lateral malleolus, and the tibial and ischial tuberosities. Drops were carried out in the usual way, with telemetry of muscle length and e.m.g.

The contact plate was used to trigger a photographic electronic flash unit, which had been masked except for a pinhole, and faced the camera. The latency to peak and time constant of the flash were found to be 0.5 and 2.5 ms, respectively, when calibrated with a photodiode.

Frame-by-frame analysis of the films was subsequently performed using the frame in which the flash was first visible as a reference, and the ms markers on the side of the film to define elapsed time.

*Local anaesthesia.* For two cats in 3 sessions, drop trials were conducted after thorough local anaesthesia of the left plantar cushion. To achieve this, light general anaesthesia was induced via the jugular catheter using methohexitone (Lilly, 3 mg/kg). Anaesthesia was then maintained for *ca.* 10 min using Halothane. Lignocaine was injected subcutaneously into the plantar cushion after the method of Engberg (1964), so that each footpad was slightly swollen with the underlying solution. The cats rapidly awoke, so that after 15 min no ataxia was visible in their gait. Local analgesia of the footpads was tested by pricking with a sterilized needle before and after the ensuing free-fall trials. A complete absence of response to such testing was taken as firm evidence of cutaneous insensibility.

Behaviourally, the cats adapted to the novelty of an anaesthetic foot within the first few min. Gait was indistinguishable from normal after this time, and no lateral imbalances were observed in falling and landing. Drop trials commenced from between 25–35 min after lignocaine infiltration.

*Movement artifacts.* Particular attention was paid to the possibility of spurious transients occurring in the e.m.g. due to (i) movement of the uninsulated segments of the e.m.g. electrodes, (ii) movement of the insulated segments subcutaneously, (iii) jolting of the telemeter after landing.

The following tests indicated that spurious signals generated in these three ways were at least an order of magnitude smaller than the mean e.m.g. amplitude encountered during the free-fall trials.

(i) In the conscious animal, a small disk of aluminium foil, connected by a fine wire to a trigger device, was stuck to the skin over the plantar surface of the foot half way along the metatarsals. With the cat lying on its side, brisk taps applied to this disk with a metal rod caused rapid dorsiflexion of the ankle. The trigger impulse thus generated, together with telemetered e.m.g. and muscle length, were stored on analogue tape.

The animal was now deeply anaesthetized with i.v. methohexitone (see above); muscle relaxation was effected with i.v. succinylcholine (200  $\mu$ g/kg), and the animal was passively ventilated. Brisk taps to the metatarsals were now repeated.

Fig. 1A shows the e.m.g. of the lateral gastrocnemius and monitored length during free fall and landing from a ht. of 0.4 m. The moment of contact by the foot is shown by the upward arrow. Fig. 1B shows the responses to a brisk tap to the foot, applied while the cat was lying on its side in a relaxed state. Fig. 1C shows the responses to a tap in the deeply anaesthetized paralysed condition.

Ignoring for a moment the slight delay after contact of the onset of stretch in Fig. 1A, it is apparent that the small artifact visible in the e.m.g. of Fig. 1C, just after contact, is negligible when compared with the corresponding e.m.g. activity in the other two cases. This is despite the greater velocity of stretch in Fig. 1C.

Such artifacts would be expected to be maximal at the highest velocities of stretch and, during the drop trials to be described in this paper, stretch velocities never exceeded those shown in Fig. 1C.

(ii) In one cat, 21 d post-operatively, and after many free-fall trials had been conducted, the e.m.g. wires were withdrawn from the lateral gastrocnemius during a brief period of general anaesthesia. A 10 k $\Omega$  miniature resistor (Plessey Riverohm)

was soldered between the ends of the wires, and exposed surfaces were coated with Dow Corning 630 surface protector and 382 medical grade elastomer. The now completely insulated and resistively coupled wires were placed alongside the muscle in approximately their former position. The skin incision was sutured closed, and the usual post-operative procedures were applied.

Free-fall trials, 1 week later, revealed that small artifacts could occasionally be seen in the otherwise silent 'e.m.g.' traces, but only at latencies longer than 60 ms

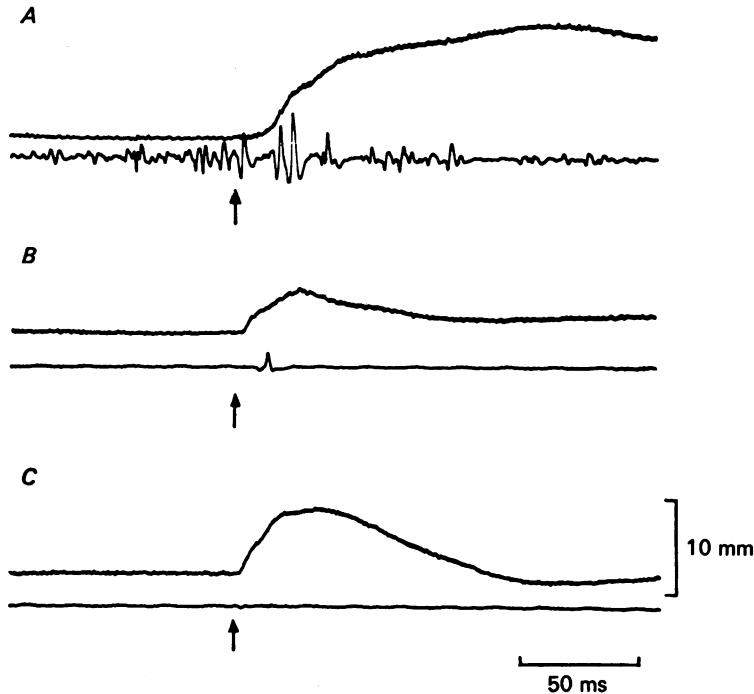


Fig. 1. *A*, monitored length (top trace) and e.m.g. (bottom trace) of lateral gastrocnemius during free fall and landing from 0.4 m. Moment of foot contact shown by upward arrow. Note delay after contact of onset of lateral gastrocnemius stretch. Lateral gastrocnemius e.m.g. shows decreased amplitude between 8 and 16 ms after contact, and then a large burst of activity (stretch response). *B*, responses to a brisk tap to the plantar surface of the foot (cat lying on side, awake). Hammer contact indicated by arrow. Tendon jerk response is evident in lateral gastrocnemius e.m.g. *C*, same as *B*, after i.v., succinylcholine during deep anaesthesia. Movement artifact in e.m.g. is negligible (same e.m.g. gains throughout).

after foot contact. Such artifacts were attributed to the jolting of the telemeter as the deceleration of the head of the cat became appreciable (Watt, 1976).

These tests did not reveal any artifacts which could be attributed to subcutaneous movement of the insulated segments of the e.m.g. wires.

In one session, the radio transmitter was replaced by wires leading directly to a Tektronix FM 122 amplifier. E.m.g. responses to landing, thus recorded, were found to be indistinguishable from those recorded by telemetry.

*Dynamic response of the length gauges.* The free-fall trial of Fig. 1A demonstrates a feature of the muscle length signals which was initially rather puzzling. There was a considerable delay (usually *ca.* 8–9 ms for a landing from 0.4 m) between the moment of foot contact and the first significant increase in monitored length.

On checking the frequency response of the length monitoring system by vibrating the length gauge longitudinally through 5 mm, and comparing the phase of the transmitted and decoded length signal with an impulse generated by a microswitch at the peak of lengthening, it was found that the phase lag was 1 ms at 100 Hz and 2 ms at 200 Hz. The amplitude frequency response was 3 dB down at 120 Hz.

Furthermore, when brisk taps to the metatarsals caused the dorsiflexion (e.g. Fig. 1B, C), the delay was only 2 or 3 ms. This was therefore the max. delay which could be attributed to the length monitoring system.

As will be shown later, high-speed filming revealed that, immediately after foot contact, toe dorsiflexion takes place, and it is only after 8–10 ms that the ankle begins to dorsiflex.

*Computation.* For most trial sequences, the rectified e.m.g. and length traces were later averaged using a DEC PDP-11/40 or a DEC PDP-8 digital computer. In the former case, the averaging programme (written by A. Handby & R. B. Muir) stored in-coming data in a push-down memory buffer so that pre-trigger as well as post-trigger times could be averaged. To achieve this with the PDP-8, a second tape recorder was used as an analogue delay line. The PDP-8 averaging programme was written by G. Malachowski & P. Crosby, and allowed editing of the occasional trial in which cross-talk from the e.m.g. to the length channel had occurred in the telemeter.

The original e.m.g. was limited to a band of frequencies between 100 Hz–2.2 kHz (60 dB/dec. roll-offs). Analogue to digital sampling rates of 5 kHz were used on both computers.

## RESULTS

*Electromyography.* Fig. 1A shows the full sequence of lateral gastrocnemius e.m.g. changes, from the moment of the fall (occurring about 250 ms before landing) to the moment of foot contact and beyond. During the fall, the e.m.g. increased progressively before contact, to be inhibited shortly after contact, followed by alternating increases and decreases in activity.

The decrease in amplitude of lateral gastrocnemius e.m.g. started at *ca.* 8 ms after foot contact, and was followed by large e.m.g. potentials commencing at 16 ms after foot contact (some 8 ms after the first significant rise in the length record).

These changes are best seen in the averaged responses of Fig. 2 where, in addition, the effects of different heights of drop are illustrated. Fig. 2 shows averages computed on the PDP-11/40 of lateral gastrocnemius e.m.g. and length responses for free-fall trials from 0.3, 0.4 and 0.5 m. In each case, 50 trials were averaged, the responses being centred around the moment of foot contact (upward arrows).

The delay after contact of the initial increase in monitored length was 11 ms for the 0.3 m falls, and 8 ms for the higher falls. In each case, at a

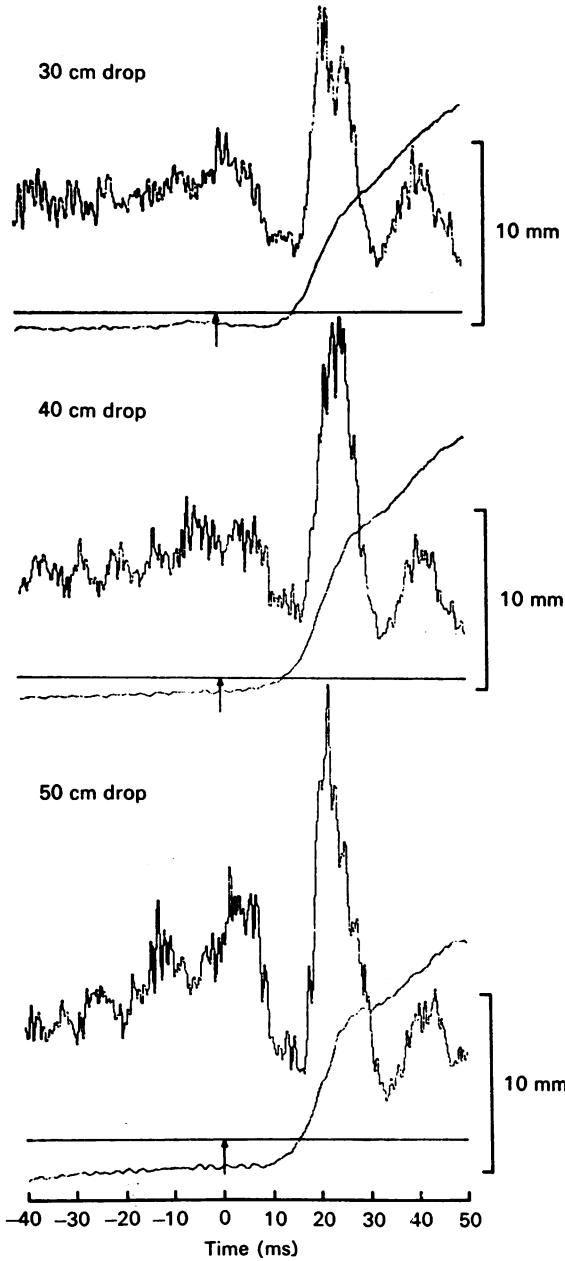


Fig. 2. Averages of rectified lateral gastrocnemius e.m.g. and length responses for drops from 3 hts., each involving 50 trials. The delay after contact of the on-set of stretch was longer for the smallest ht. At 8-9 ms after contact, lateral gastrocnemius e.m.g. amplitude decreased in each case. This was followed by large peaks with on-set at ca. 8 ms after beginning of stretch. A further peak occurred at 40 ms after contact. Note that the length changes were not significantly different, indicating effectiveness of c.n.s. compensation (e.m.g. at same gain throughout).

latency of 8–9 ms, the e.m.g. amplitude rapidly decreased. This was followed (*ca.* 8 ms after the onset of length increase) by a large peak of activity lasting some 20 ms, and a further peak at *ca.* 40 ms after foot contact.

The build-up in e.m.g. prior to foot contact is consistent with the findings of Watt (1976), and indicates a correlation between the height of the fall and amplitude of pre-landing e.m.g. The relative constancy of muscle length during this build-up suggests that the antagonist muscles were co-contracting in order to stiffen the joint for the impending torque transients.

The responses after landing suggest that, prior to any detectable ankle rotation, there was an inhibition of lateral gastrocnemius motoneurons. An excitation then occurred, apparently in response to stretch of the muscle.

Because the latencies of excitation after the onset of stretch were similar to those seen in tendon jerks and rapid passive stretches (Fig. 1*B*), it seems reasonable to assume that at least the early part of the excitation was monosynaptically mediated.

*Cinematography.* At this stage it was felt necessary to arrive at a closer understanding of the changes in joint angles which take place before and after landing.

Fig. 3 shows the outlines of the left hind limb of a cat falling from 0.4 m, traced from selected frames of a 1400 frames/s cinematograph film. The no. beneath each tracing indicates the time in ms, relative to foot contact, appropriate to that particular frame. Between 0 and 11.2 ms after contact, more tracings are included to define in a better way the joint angles during this period and, for clarity, alternate tracings appear as broken lines.

The dot within each outline shows the position of the skin marker over the lateral malleolus. In order to obtain estimates of the length ( $L$  in Fig. 3, insert) from a fixed point  $d$  on the dorsal surface of the calcaneum to a fixed point over the lateral epicondyle of the tibia  $b$ , the following geometrical procedure was applied.

It was assumed that negligible skin slippage occurred over the lateral malleolus (point  $c$ ), that the length  $cb$  measured along the tibia from the lateral malleolus to the lateral epicondyle of the tibia (85 mm) remains constant and that the arc  $ab$  (with centre of rotation  $c$ ), intersects the ventral outline at a region where the tibia lies immediately subcutaneously. Thus, a 15 mm arc drawn dorsad from  $a$  defines  $b$ . The intersection of tangents to the plantar surface of the foot and the surface overlying the tendons of the triceps surae defines point  $d$ .

It should be noted that the length  $L$ , thus derived, represents most accurately the length of the portions of the ankle extensors which have their origin at the head of the fibula, and less accurately those which originate from the femur. The same is true for the signals monitored from the implanted length gauge.



The graph of Fig. 3 shows the variations in the estimated length  $L$  for a single drop relative to the moment of foot contact (time 0).

It is apparent that the first significant increase in  $L$  after landing occurred at a latency of between 8.4 and 11.2 ms. Closer examination of the tracings shows that, during this time, the toes are rapidly dorsiflexed.

*Foot-pad anaesthesia.* It was felt that the early depression of lateral gastrocnemius e.m.g. (commencing between 8 and 9 ms after foot contact) could have been due to convergence from toe extensor afferents (Laporte

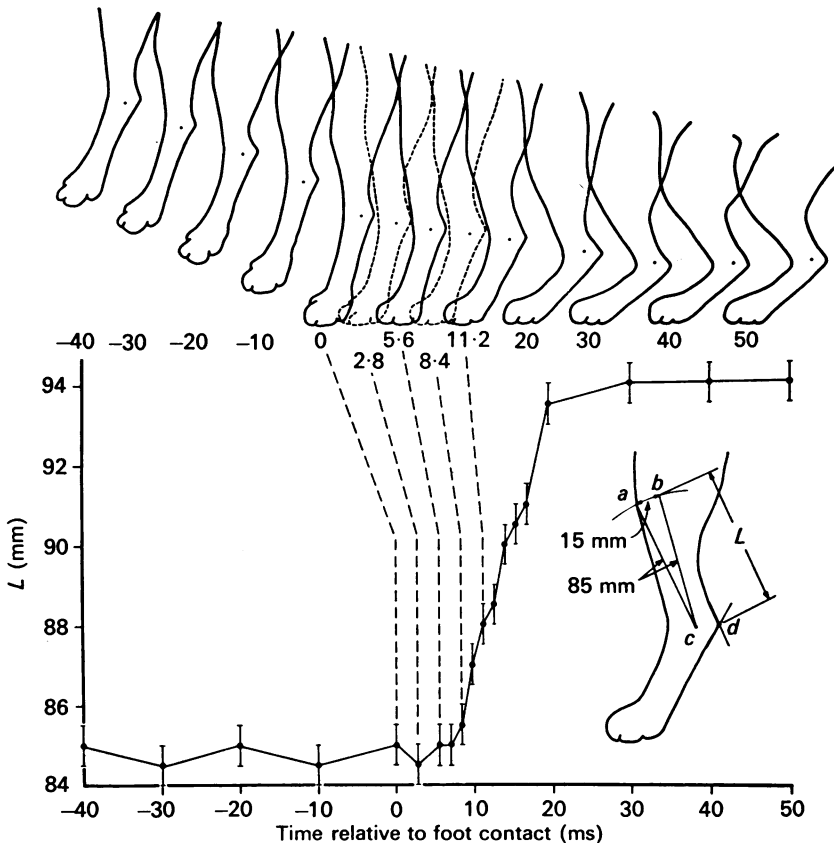


Fig. 3. *Top*: tracings of outline of left hind limb taken from ciné film (0.4 m drop). The no. below each tracing indicates time (ms) relative to foot contact appropriate to that tracing (- pre-contact, + post-contact). Dots show position of lateral malleolus. Between 0 and 11.2 ms, more frames are included, alternate tracings shown as interrupted lines for clarity. *Bottom*: plot of length  $L$  from calcaneum to head of tibia (derived from the tracings) vs. time relative to contact. *Insert* shows geometrical construction used to obtain  $L$  using reference points  $c$  and  $d$  (see text).  $L$  shows a significant increase from between 8.4 and 11.2 ms after foot contact.

& Lloyd, 1952; Eccles, Eccles & Lundberg, 1957*a, b*), and cutaneous and joint afferents (Lundberg, Malmgren & Schomburg, 1975).

To more closely identify the afferent source of the apparent inhibition, local infiltration of lignocaine into the plantar cushion was carried out as described above in two cats.

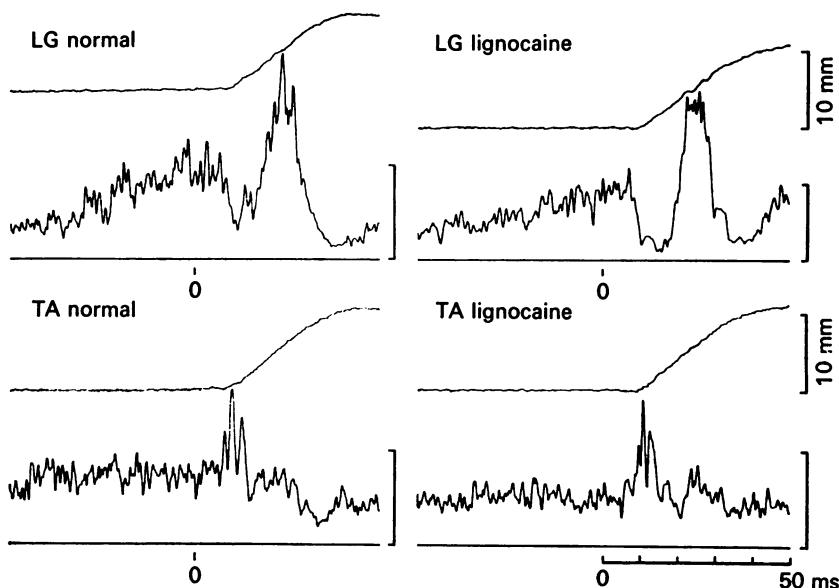


Fig. 4. Averages of four free-fall sequences, each involving thirty-six drops. *Left*: e.m.g. responses of lateral gastrocnemius and tibialis anterior under normal conditions (length refers to triceps surae in all cases). *Right*: same, after local anaesthesia of left foot-pads. No significant differences in overall pattern are evident between left and right pairs (for computational reasons, nominal unit of e.m.g. calibration in top right record is slightly smaller. LG = lateral gastrocnemius. TA = tibialis anterior.

Fig. 4 shows the averages computed on the PDP-8 of four free-fall sequences, each involving thirty-six drops. On the left are the plotted averages for monitored length and the e.m.g.s from lateral gastrocnemius and tibialis anterior before paw anaesthesia. The decrease in amplitude of lateral gastrocnemius e.m.g. starts some 8.5 ms after foot contact. At about the same latency, there is an increase in tibialis anterior e.m.g.

After foot-pad anaesthesia, no significant changes were evident in the reflex patterns, either in terms of amplitude or latency (note that the top right-hand e.m.g. calibration differs from the other three). The averaged results from both cats for three sessions (totalling 350 free-fall trials after local anaesthesia) support this negative finding.

## DISCUSSION

The foregoing results strongly suggest that, in the 50 ms after landing from a fall, complex but characteristic patterns of reflexes evolve in cat ankle muscles.

Greenwood & Hopkins (1976*b*) found that, when the height of a downward step was unexpectedly increased, the e.m.g. stretch responses in human soleus were delayed, indicating that they were indeed stretch responses, and not 'pre-programmed' activity generated by prediction.

Similarly, in our free-fall trials, the responses were too clearly correlated with landing to support the latter idea.

It would seem inappropriate to try to equate the various components of the reflexes to the well known 'long-loop', or functional stretch reflexes, seen during single-joint perturbations in other species. The landing reflexes, no doubt, result from the convergence of afferent and supraspinal influences, which become progressively more difficult to unravel as the movements develop. The present results only allow speculation as to the origin of the very early components of e.m.g. response with latencies which would preclude supraspinal integration.

*Initial inhibition.* The first lateral gastrocnemius response after contact was a brief reduction in e.m.g. activity. The rapidity of this response (8–9 ms) indicates a segmental inhibition of lateral gastrocnemius motoneurons superimposed on the gradually increasing pre-contact excitability.

We propose that the inhibition is largely the result of the nett action of stretch-evoked activity of afferents from muscle (and possibly joint) receptors of the foot. The further possibility of autogenetic inhibition by triceps surae tendon organ afferents will also be considered.

The first alternative is suggested by the extreme rapidity of dorsiflexion of the phalanges in the first few ms after contact (Fig. 3). The trials in which the plantar cushions were anaesthetized would seem to rule out the involvement of cutaneous afferents, at least those innervating the foot-pads.

Some inhibition might indeed have been expected from these afferents, as Engberg (1964) observed regularly IPSPs in ankle extensors evoked by pad stimuli. The threshold for this effect, however, was high, and in the same study it was reported that anaesthesia of the plantar cushion had no detectable effect on the e.m.g. patterns of plantar muscles in the step cycle of conscious cats.

What, then, are the actions of non-cutaneous afferents of the foot on ankle extensor motoneurons?

Laporte & Lloyd (1952) showed that, in the unanaesthetized decapitate

cat, there was a disynaptic inhibitory effect on triceps surae motoneurons from flexor digitorum longus group I afferents, and a parallel excitatory effect on tibialis anterior motoneurons.

Similarly, Eccles *et al.* (1957*b*) found that in barbiturate-anaesthetized spinal cats, flexor digitorum longus afferents were particularly effective in evoking disynaptic inhibitory actions in gastrocnemius-soleus motoneurons. Indirect evidence strongly suggested that Ib afferents were responsible.

In the unanaesthetized, ischaemically decerebrated spinal cat, stretch of flexor digitorum longus has recently been shown by monosynaptic testing to inhibit consistently soleus motoneurons and inconstantly (but often fairly strongly) inhibit gastrocnemius motoneurons (Yeo, 1976). Afferents of Pacinian corpuscles of the interosseus membranes are unlikely to contribute to triceps surae inhibition (Yeo & McIntyre, 1976).

The heteronymous reflex actions of afferents of the intrinsic foot muscles are poorly understood but, by analogy with flexor digitorum longus, tendon organ afferents of the lumbricals and short flexors might be expected to support the observed inhibition. Afferents from the toe extensors, interossei and the various joint capsules of the foot may also influence the response.

As suggested above, a further source of inhibition of lateral gastrocnemius might originate from activity of tendon organ afferents of the ankle muscles themselves. Newsom Davis & Sears (1970) observed a short-latency inhibition of intercostal e.m.g. as a result of imposed muscle stretch in man, and attributed this to the autogenetic action of tendon organ afferents. The increase in muscle activity prior to landing in our experiments is closely analogous to a similar increase during voluntary expiration in the intercostal study. The patterns of inhibition followed by excitation, after the perturbations, are also closely similar.

There is, however, one difficulty in applying the same interpretation to the present results. The lack of a detectable lengthening of the ankle extensors in the first 8 ms after foot contact would argue against an early activation of their stretch receptors.

Indeed, we investigated this directly by replaying, from analogue tape, the recordings of three spindle primary afferents of the ankle extensors, whose discharges had been monitored during falling and landing in the conscious cat (Prochazka *et al.* 1977). Close examination of ten trials showed that the first increase in rate of spindle discharge came at an average of 0.2 ms after the first increase in monitored length. Given the inherent 2 ms delay in the length monitoring system, this would be consistent with the responses having resulted from the first observed increase in muscle length.

On the other hand, the considerable lateral gastrocnemius e.m.g. activity at the moment of foot contact implies a high level of stiffness

about the ankle joint. Assuming that the torque generated about the ankle pivot during the initial period of rapid toe dorsiflexion is relatively small, it is possible that the resulting changes in length would be smaller than the resolution of the length monitoring system (*ca.* 0.5 mm). Thus, ankle extensor tendon organ discharge in the first 8 ms, and therefore the possibility of autogenetic inhibition, cannot be excluded.

Delays in the onset of ankle rotation, similar to those reported here, were noted in the human experiments of Melvill Jones & Watt (1971*a*), and were presumed by these authors to be associated with an initial dorsiflexion of the toes. The possible conditioning action of afferent input from this first perturbation on the subsequent responses of ankle extensor motoneurons was not discussed.

In this context, it may be worth while noting that, in the experiments of Greenwood & Hopkins (1976*b*) where, contrary to Melvill Jones & Watt (1971*a, b*), stretch reflexes in the ankle extensors were observed, the subjects wore shoes. Unfortunately, the extent to which toe dorsiflexion was thereby prevented was not stated.

*Excitation.* Following the initial depression of lateral gastrocnemius e.m.g., the rapid increase in amplitude is at a latency which suggests a monosynaptic response to stretching. The increased excitability, however, endures for some 20 ms, and is in this respect unlike the rapid monosynaptic component of e.m.g. response to perturbations about a single joint (e.g. Evarts & Tanji, 1974).

On the other hand, this peak of e.m.g. activity is very similar to that in the decerebrate stretch reflex (Nichols & Houk, 1976).

In view of the short latency of the response with respect to muscle stretch, it is presumed that group Ia afferent activity mediates the increased motoneuronal discharge.

The size of the excitatory response increases with the height of the drop (e.g. Fig. 2). This is, no doubt, partly due to the increased velocity of stretch, causing higher spindle afferent firing rates. Additionally, the 'gain' of the stretch reflex may have increased with the higher levels of prior motoneuronal activity (Newsom Davis & Sears, 1970). It is interesting that the extent of the initial inhibition is similarly related to the height of the drop.

*Functional significance.* From a descriptive point of view, the present results confirm that the activity in lateral gastrocnemius builds up prior to contact (Watt, 1976), and there is every reason to believe that this anticipatory activity is essential for a controlled landing (Watt, 1976; Greenwood & Hopkins, 1976*a, b*).

Sears (1974) suggested that the initial inhibitory response of intercostal muscles to stretching might 'allow the subsequent phase of the reflex action to be matched in sign and intensity to the voluntary movement occurring consequent on perception of the unexpected load'.

The initial inhibition of lateral gastrocnemius after foot contact observed by us may similarly serve to enhance the response to the subsequent stretch. It is feasible that, by inhibiting the firing of a proportion of the active motoneurons for *ca.* 10 ms, a greater synchronization of stretch-evoked firing might then be achieved at precisely the time at which it is most needed.

In our recordings, the peak of lateral gastrocnemius response after landing occurred between 15–20 ms after the onset of muscle stretch. Indeed, the e.m.g. pattern during the period of stretching is very similar in form to that recorded from cat soleus in the decerebrate stretch reflex (Nichols & Houk, 1976).

In their elegant analysis, these authors showed that this reflexly-mediated peak of e.m.g. was associated with a dramatic increase in the stiffness of the lengthening muscle, in comparison with that of a muscle under steady motoneuronal drive, at least at rates of stretch up to 85 mm/s.

Tatton, Forner, Chambers & Liu (1975) showed that, when a short-latency component of the stretch response was absent in monkeys with cortical lesions, early tension production in response to perturbations was delayed, and corrections were therefore slower.

Along similar lines, Nashner (1976) reported that subjects who had strong functional stretch reflexes showed a more rapid stabilization of sway during stance perturbations than those in whom these reflexes were not present.

In conclusion, our results indicate that, after landing from a fall, large and rapid reflexes occur in cat ankle muscles. The length of the ankle extensors starts to increase only after considerable dorsiflexion of the toes has taken place. The excitability of the ankle extensor motoneurons, after foot contact, would appear to be strongly influenced by the convergent action of non-cutaneous afferents responsive to toe dorsiflexion. An initial autogenetic inhibition is not excluded. A stretch-evoked peak of activity occurs soon enough for the resulting active tension to contribute significantly to the extensor force involved in deceleration after landing.

We thank Professors A. K. McIntyre, R. Porter, T. A. Sears and A. Taylor and Drs D. Burke, U. Proske, K. H. Sontag and J. A. Stephens for helpful suggestions. We are indebted to Messrs D. C. Hauser, R. Crompton and M. Ryan for the high-speed cinematography, and to D. J. Dewhurst for use of the PDP-8 computer. This project was supported by the Australian Research Grants Committee, grant no. D1-75/15084 and the PDP 11/40 computer was that provided by the A.R.G.C. for work in Professor Porter's laboratory.

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