

HINDLIMB MUSCULAR ACTIVITY, KINETICS AND KINEMATICS OF CATS JUMPING TO THEIR MAXIMUM ACHIEVABLE HEIGHTS

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SUMMARY

Cats were trained to jump from a force platform to their maximum achievable heights. Vertical ground reaction forces developed by individual hindlimbs showed that the propulsion phase consists of two epochs. During the initial 'preparatory phase' the cat can traverse many different paths. Irrespective of the path traversed, however, the cat always attains the same position, velocity and momentum at the end of this phase. Starting from this dynamic state the cat during the subsequent 'launching phase' (about 150 ms long) generates significant propulsion as its hindlimbs develop force with identical, stereotypic profiles. Cinematographic data, electromyographic data, and computed torques about the hip, knee and ankle joints indicate that during the jump proximal extensor musculature is activated before distal musculature. During terminal experiments when the hindlimb was set at positions corresponding to those in the jump, isometric torques produced by tetanic stimulation of groups of extensor and flexor muscles were compared with computed torques developed by the same cat during previous jumps. These comparisons suggest that extensor muscles of the hindlimb are fully activated during the maximal vertical jump.

INTRODUCTION

There is recent interest in the biomechanics and the neural control of locomotion of cats and other animals (Grillner, 1975; Herman *et al.* 1976). The study of intact cat locomotion is complex due to, for example, interlimb co-ordination in addition to co-ordination of musculature within a given limb. There are however preparations that facilitate studies on limb coordination in mammalian locomotion (see reviews, Grillner, 1975; Orlovsky & Shik, 1976; Wetzel & Stuart, 1976). Vertical and forward jumping is another important movement in the cat's repertoire with advantages for

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experimental study. These jumps presumably require bilateral synchronized movement of the hindlimbs with little forelimb participation during propulsion. As a result no complex interlimb timing is expected and analysis of intralimb muscular coordination can be emphasized without regard to constraints imposed by the other limbs. Cats can be trained to jump to maximum vertical heights (Zomlefer, Zajac & Levine, 1977) and onto high tables (Smith *et al.* 1977; Walmsley, Hodgson & Burke, 1978), while instrumented in order to obtain kinetic, kinematic and electromyographic data. Such data is useful for comprehension of the biomechanics and neural control of jumping of intact animals. Since the kinematics of the jumping cat is similar to that which occurs during locomotion, and especially during galloping (Goslow, Reinking & Stuart, 1973; Miller, Van der Burg & Van der Meche, 1975), a study of jumping should provide insight to our understanding of locomotion.

This paper reports results from cats jumping to their maximum achievable vertical heights. Particularly relevant to the study reported here is the general notion that maximal height jumping may be stereotypic behaviour, requiring maximum activation of muscles and pre-programmed limb movement. Not only is this task an ideal one for experimental study but it is well suited to analytical, computer simulation and optimal control studies, i.e. the task can be theoretically formulated (Zomlefer *et al.* 1974; Zomlefer, Levine & Zajac, 1975; Roberts *et al.* 1976; Zajac & Levine, 1979). Preliminary results have been reported (Zomlefer, Zajac & Levine, 1974; Zomlefer, Zajac & Levine, 1976; Zomlefer *et al.* 1977).

MATERIALS AND METHODS

Observations were made on five adult cats (2.5–3.4 kg). The techniques used to train the animals, record electromyograms and compute hindlimb joint angles have been described elsewhere (Zomlefer, 1976; Zomlefer *et al.* 1977). Briefly, each animal was trained to jump vertically from a force platform and touch a cotton target at any height up to its maximum achievable height. Afterwards, intramuscular bipolar electromyographic (EMG) electrodes were used to simultaneously record from extensor digitorum longus (EDL), medial gastrocnemius (MG), vastus lateralis (VL) and semitendinosus (ST) during subsequent jumps from the platform. Stroboscopic techniques (67 Hz with pulse width of 0.01 ms) and low speed (60 frames/s) cinematography were used to determine the trajectories of the ankle, knee and hip joints. A high speed movie camera (Fastax model WF 4, operated at 378 frames/s with a shutter speed of about 1/1500 s) was sometimes employed to provide greater resolution and to better delineate the kinematics both during the entire propulsion phase and after lift-off. The force platform used in this series of experiments is an improvement on the earlier version (Zomlefer, 1976; Zomlefer *et al.* 1977). The new device permits vertical contact force from one hindlimb to be recorded simultaneously with the force from the other limb. The device consists of two 80 cm² force plates separated by a few mm. The frequency response of each plate is greater than 300 HZ.

Terminal experiments were conducted on two of the trained cats (2.7 and 3.4 kg) to determine their isometric torque versus joint angle relationship for the hip, knee and ankle. Anaesthesia was induced with halothane and continued with i.v. pentobarbital. Blood pressure was continually monitored. Heating pads and lamps main-

Maintained body temperature at 37 ± 1 °C. Stimulating cuff electrodes were implanted around the hamstrings nerve, the femoral nerve, the peroneal nerve and the tibial nerve. The tibial nerve was cut after its innervation of plantaris muscle. The cat was then placed in an apparatus which enabled the hindlimb to be rigidly held at any physiological combination of hip, knee and ankle angles. The ilium was immobilized by clamps on the iliac crest and on the ischium proximal to its tuberosity. Pins were inserted into the distal femur and the talocrural joint to immobilize the thigh and leg as appropriate for torque measurements around each of the joints. The pin in the femur was placed in a direction which followed the fascial planes of the muscles to minimize disturbances to muscular contractions of the quadriceps and hamstring muscles. Each nerve was stimulated with supramaximal pulses of 50 μ s duration at rates up to 100 pps for 0.5–1.0 s. Few trains were given and no more frequently than once per 2 min to prevent muscular fatigue. A semiconductor strain-gauge transducer was placed perpendicular to the foot, leg and thigh to measure isometric extensor (and at times flexor) torque about the ankle, knee and hip, respectively. The hindlimb joint angles were matched to those occurring at various times during previous jumps by the same animal. Location of the chronically implanted EMG electrodes and anatomical measurements were made post mortem.

RESULTS

Vertical ground reaction force on each hindlimb

All cats developed vertical force in a way that permitted the propulsion phase of the maximum jump to be classified into two epochs (Zomlefer *et al.* 1977). During the first epoch ('preparatory phase') the total vertical force exerted by the cat's two hindlimbs is variable from jump to jump, but during the second part ('launching phase') the force is stereotypic [e.g. in Fig. 2 (top) compare the variability in force curves prior to point B with the stereotypy in curves after point B]. Vertical contact forces produced by the individual hindlimbs of a given cat are consistent with this two-phase schema. As an example of the variability occurring in the preparatory phase, one cat in some jumps would alternate his body weight from one foot to the other (Fig. 1 B) and in other jumps the cat developed similar force trajectories (Fig. 1 A). In all jumps the force developed by one hindlimb during the launching phase was about equal to the force developed by the other hindlimb (Fig. 1 A and 1 B). Lift-off times (point D) for the two hindlimbs did not usually differ by more than 5 ms.

The vertical force impulse (net area under the force-time curve minus contribution due to body weight) equals the animal's vertical momentum at lift-off. The contribution to force impulse by the launching phase was about 75% of the total force impulse due to, in part, the high peak force ($4\text{--}5 \times$ body weight) occurring just after heel-off. Most of the vertical momentum generated at lift-off is therefore a result of the stereotypic launching phase.

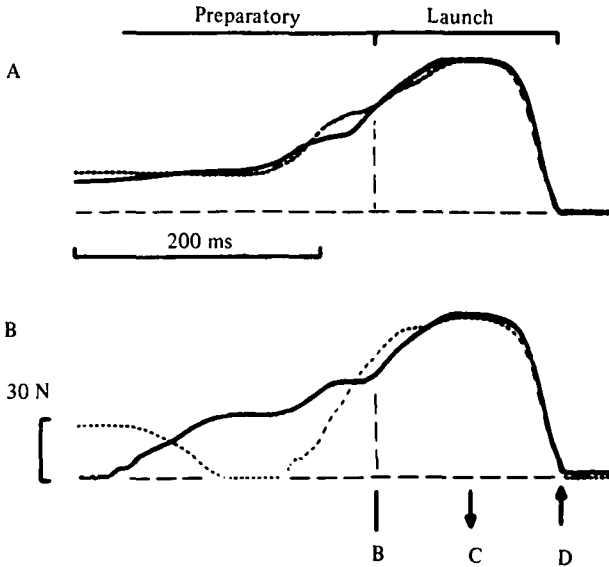


Fig. 1. Vertical ground reaction forces produced by the hindlimb during two jumps by a cat to its maximum achievable height. Contact forces by each hindlimb (left limb: solid curve; right limb: dashed curve) are nearly identical in both jumps during the launching phase (time epoch B–D). During the preparatory phase (time epoch prior to B) the contact forces could be similar (A) or different (B). Heel-off occurs at time C and lift-off at time D. The combined vertical contact force from both hindlimbs was variable from jump to jump during the preparatory phase and identical during the launching phase (Fig. 2, top). Animal body weight is 33.4 N. Target was placed 1.18 m above platform and was touched by the cat's nose. Net vertical impulse during preparatory phase = 11 N s and during launching phase = 4 N s.

Muscular activation and kinematics of the hindlimbs

In Fig. 2 are shown the total vertical force produced by both hindlimbs, the EMG records from VL, ST, MG and EDL muscles, and the kinematics of the left hindlimb. ST activity began in the preparatory phase and preceded VL and MG activity. ST activity also ceased before that of VL and MG, with cessation beginning at a time about equal to peak force. The onset of ST activity was less regular than that of either VL or MG. VL activity began abruptly at the beginning of the launching phase and abruptly terminated 20 ms before lift-off. There was some activity in MG during the latter part of the preparatory phase and during the early part of the launching phase. However, an increase in MG activity appeared later and during most of the launching phase. MG activity ended abruptly at a time about coincident with cessation of VL activity. The onset and offset times of EDL activity were variable from jump to jump in contrast to the consistency in EMG behaviour of the other three muscles. However, EDL activity was always present during the entire launching phase.

Kinematics obtained from high speed cinematography indicate that during propulsion the hip angle is initially at 90° , begins its monotonic extension in the preparatory phase, and continues to extend during the launching phase until a maximum extension of 175° is reached. The knee angle also undergoes a continual extension during the jump. During the preparatory phase the knee angle is first in a flexed position (about 45°) and then during the launching phase the knee extends until at lift-off an

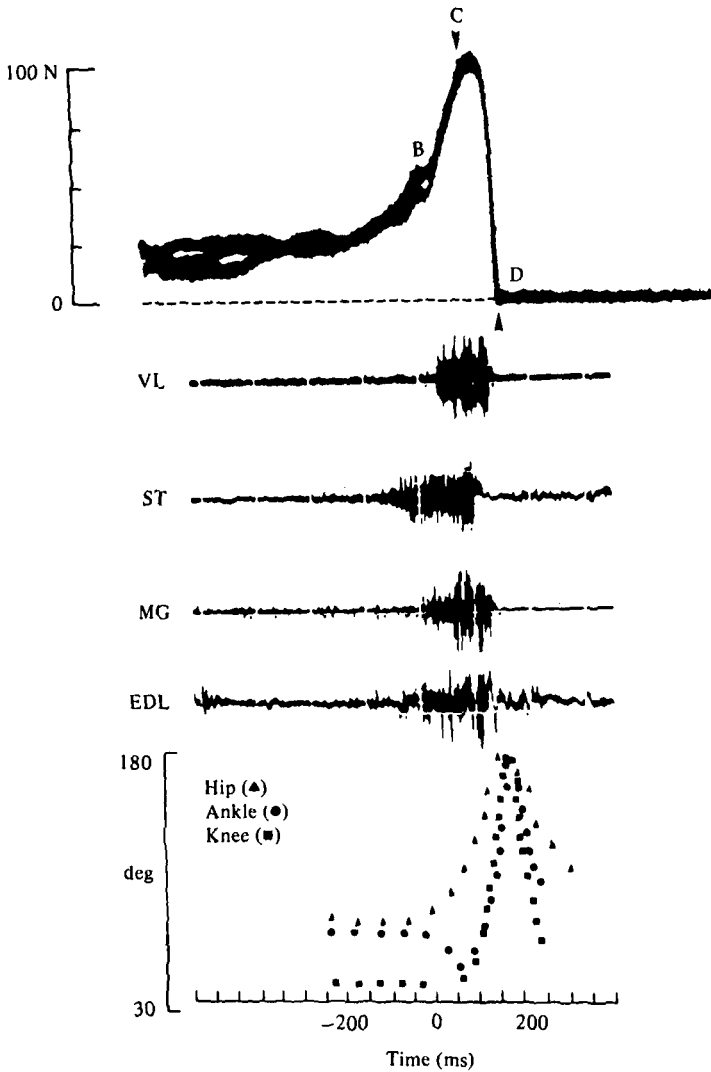


Fig. 2. Vertical force, electromyographic (EMG) activity of four hindlimb muscles and hind-limb kinematics recorded from a cat during a jump to its maximum height. Top: superimposed traces of the total vertical reaction force developed by both hindlimbs in five 'maximal' jumps. Notice that the vertical force can vary from jump to jump during the first part of the jump (i.e. the 'preparatory' phase) and is stereotyped during the latter part (i.e. the 'launching' phase). The time delineating these two epochs is defined at point B. Instants C and D indicate heel-off and lift-off. Middle: EMG activity recorded from vastus lateralis (VL), semitendinosus (ST), medial gastrocnemius (MG) and extensor digitorum longus (EDL). EMG activity from EDL muscle was previously reported (Zomlefer *et al.* 1977) as that emanating from tibialis anterior muscle. Post-mortem study of this and other animals showed that the electrodes were however implanted in EDL muscles. Bottom: hip (▲), knee (■) and ankle (●) joint angles. Cat weight = 25 N.

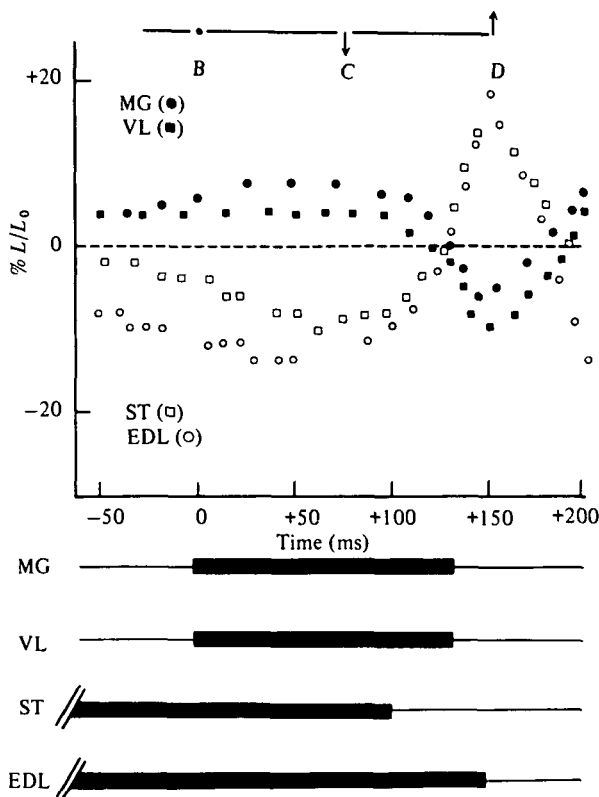


Fig. 3. Length trajectories of four hindlimb muscles during the jump. Top: changes in lengths of VL (■), ST (□), MG (●) and EDL (○) muscles relative to standing length L_0 (Goslow *et al.* 1973) for the same cat in Fig. 1. Time epoch notations above the figure are the same as in Fig. 1. Bottom: bars indicate approximate times during which maximum EMG activity from MG, VL and ST occur and the usual time during which EDL was active.

angle of 160° is reached. In contrast, the ankle angle is initially at 80° in the preparatory phase and it then flexes to 60° during the launching phase. Flexion stops at about heel-off and then the ankle angle follows an extension trajectory similar to that of the knee.

The percentage change of lengthening and shortening (relative to standing length of MG, TA, VL and EDL (Fig. 3) were computed using the trigonometric relations discussed by Goslow *et al.* (1973). Prior to heel-off, MG is at a length greater than resting and is stretched at a rate of about 100 mm/s ($1.0 L_0/\text{s}$), which is a lengthening rate between that which occurs in the 'yield' phase of walking (78 mm/s) and that of trotting (120 mm/s) (Goslow *et al.* 1973). In contrast, VL is isometric at a length also greater than resting. During the latter part of the launching phase from heel- to lift-off, both MG and VL shorten rapidly 260 mm/s or $2.6 L_0/\text{s}$, and 325 mm/s or $3.8 L_0/\text{s}$, respectively). Since both MG and VL are active during the whole launching phase, the overall contraction in MG is thus an 'active stretch-shorten' one whereas that in VL is an active isometric-shorten contraction. The simultaneous occurrence of these different types of contractions in MG and VL during jumping is antithetical to the

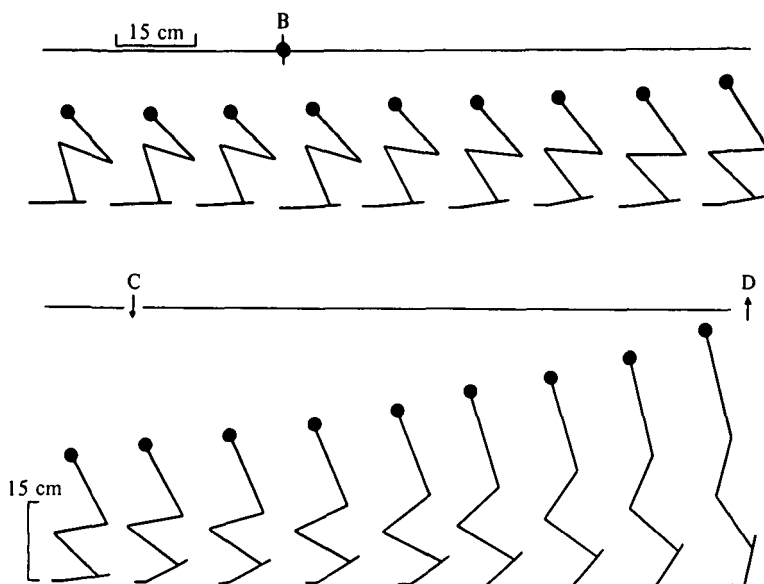


Fig. 4. Stick figure diagrams to show progression of the cat during the maximal vertical jump. For biomechanical analysis and modelling (Zajac & Levine, 1979) the cat is represented as a four-segmented animal (i.e. trunk, thigh, leg and foot). As a first approximation the toes can be neglected (Zajac & Levine, 1979) and are only shown for clarity and completeness. Beginning of the launching phase is depicted by point B, heel-off by C (\downarrow) and lift-off by D (\uparrow). No detection of body movement was evident prior to the top left-most stick figure. Lift-off occurs 16 ms after right stick figure. Time between stick figures, which are drawn from cinematographic records, is 21 ms. Centre of mass of trunk was calculated from each cinematographic frame and was assumed to be at a position half the distance from the atlanto-occipital joint to the acetabulum. Notice that the centre of mass (c.m.) of the trunk (large dot at top of each figure) moves forward and upwards about the same amount prior to heel-off and then the c.m. moves principally upwards. This cat's c.m. moved horizontally during propulsion and in flight more than any other cat. Notice that the thigh and foot are the only two segments which rotate significantly (about 90°) and that the thigh begins its rotation first. Same animal as in Fig. 1.

occurrence of similar types (active stretch-shorten contractions) in MG and VL during walking. Apparently the presence of a yield phase (e.g. Goslow *et al.* 1973) is fundamental to the similarity of muscular contractions in MG and VL during walking.

The length trajectories of ST and EDL are similarly shaped and complementary to those of the ankle and knee extensors. ST and EDL are below rest length throughout the launch phase except for a short time preceding lift-off. Prior to heel-off they shorten (88 mm/s or $0.7 L_0/s$, and $0.6 L_0/s$, respectively) and after heel-off they rapidly lengthen (430 mm/s or $3.6 L_0/s$, and $4.3 L_0/s$, respectively). Since EDL is active during these periods, it must be concluded that EDL exhibits an active shorten-lengthen contraction. ST must also undergo an active shorten-lengthen contraction, though the lengthening phase is rather brief since ST becomes inactive between heel-off and lift-off. The long-lasting active shortening followed by a short-lasting lengthening contraction in ST is similar to that which occurs during walking. On the other hand, the active shorten-lengthen contraction in EDL is opposite to that which occurs during walking.

To better portray the kinematics of the hindlimbs during the propulsion phase of the

jump, stick figures were used to diagram the forward and upward motions of the ■ (Fig. 4). Only one hindlimb is represented due to bilateral symmetry in the jump. Measurements of hip, knee, ankle and digit joint angles and limb segments were used to construct the hindlimb stick figures. Notice that the femur, in comparison with the tibia, rotates considerably during the launch phase. As the launch phase progresses, this femur rotation is followed by metatarsal and then by tarsal rotation (not shown, but occurring immediately before lift-off). Such rotations, and especially femur rotation, contribute significantly to vertical movement of the centre of mass (c.m.).

Kinematics of the trunk

Fig. 4 shows the movement of the centre of mass of the trunk. Notice that there is little movement in the preparatory phase (Fig. 4, prior to B), horizontal and vertical movement in the first part of the launching phase (Fig. 4, B–C), and mostly vertical movement after heel-off (Fig. 4, C–D). The horizontal movement is due to presumed horizontal forces generated during propulsion. Calculations and preliminary observations indicate that such forces are not large in comparison to the peak vertical force developed in the jump. Notice also that trunk rotation is small in comparison with femur and metatarsal rotation.

Cinematographic analysis indicated that the trunk continuously extends during the propulsion phase and that such movement is manifested more in the launching than in the preparatory phase. For instance the length of the trunk, defined as the distance from the hip joint to the atlanto-occipital joint, increased by about 50% during the launch. This large extension is expected since the animal begins the jump in a 'crouch' and terminates its propulsion fully 'stretched'. Thus the c.m. used in Fig. 4 assumes that the ratio of the distance between the hip joint and the c.m. of the trunk to the length of the trunk is constant ($= 0.5$; Manter, 1938).

It was also verified that the jump under study in these experiments was a 'pure' vertical jump. This conclusion was based on the fact that once airborne our cats did not travel forward very far, as evident by high speed cinematography.

Kinematics of the head, forelimbs and tail

Frame-by-frame analysis of the motion pictures revealed that the cat lifted its forepaws off the ground and moved its forelimbs into a fully flexed position during the preparatory phase. Some cats would squat in the crouch with only one forelimb touching the ground and the other flexed. It is believed therefore that the forelimbs do not contribute significantly to propulsion but rather are used initially in the jump for static stabilization (see also Tokuriki, 1979). The animal's head always maintained a fixed angle relative to the target and its tail (except for the most proximal part) always pointed upward and never touched the ground. Thus neither head nor tail appear to assist in propulsion.

Torques about the hip, knee and ankle joints

The torques produced around the three joints were calculated from the vertical ground reaction force and the kinematics of the body (Fig. 5 A, B). Major assumptions are that the horizontal forces are not large and that prior to heel-off the vertical for vector acts through the c.m. of the trunk.

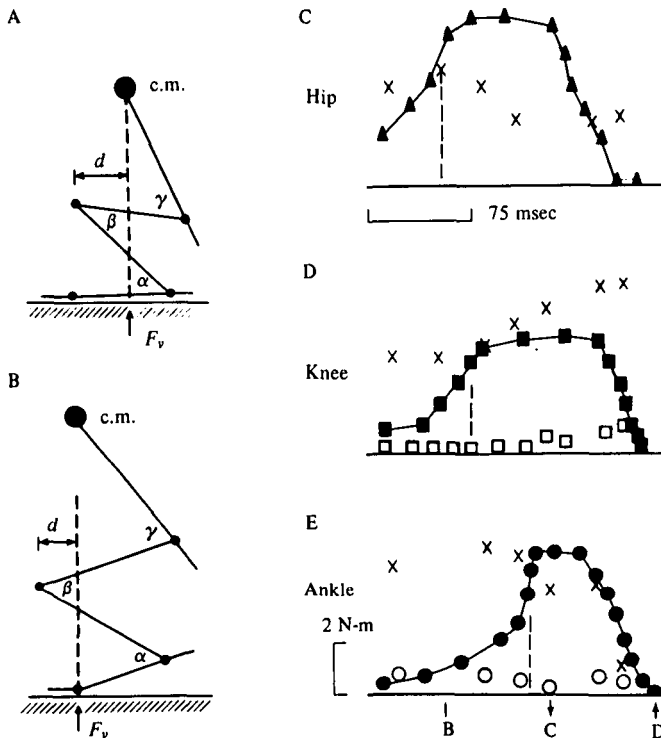


Fig. 5. Torques produced about the hip, knee and ankle joints during the maximal jump and during maximal isometric contractions of hindlimb muscular groups. (A) Stick figure with heel on the ground to show method for calculating torques about the hip, knee and ankle joints. The stick figure is constructed from one cinematographic frame. Centre of mass (c.m.) of the trunk is assumed to be half the distance from the hip joint to the atlanto-occipital joint. The vertical ground reaction force is assumed to act through the c.m. of the trunk. Knee torque is equal to $F \times d$. Other torques are calculated similarly. (B) Stick figure with heel off the ground to show method for calculating torques. Method is the same as in (A) except F_v is assumed to act through the metatarsophalangeal joint and location of c.m. is not necessary. α , β and γ are the defined ankle, knee and hip angles. (C-E) Calculated torques about the hip (\blacktriangle), knee (\blacksquare) and ankle (\bullet) joints during the jump. Each dashed line shows the time at which 80% of peak torque is reached during the jump. Electromyographic records from ST, VL and MG muscles (Fig. 2) indicate that muscles which extend these joints are activated about 50 ms prior to these times. Maximal isometric extensor torques about the hip, knee and ankle joints (\times) during supramaximal stimulation of the hamstring, femoral and tibial nerves, respectively, were obtained during a terminal experiment on the same cat with its left hindlimb set to some of those positions which it had during the jump. Maximal flexor torques about the knee (\square) and ankle (\circ) joints were obtained during stimulation of the hamstring and peroneal nerves, respectively. Isometric torques were measured at a time just prior to cessation of the 0.5 or 1.0 s stimulus trains. Same animal as in Fig. 1.

The torques produced around the hip, knee and ankle joints during the propulsion phase of the jump are at first low since they need to support only the weight of the cat in its initial crouch. Within about 50–75 ms the torques rise rapidly to attain peak values (Fig. 5 C, D, E). Notice that peak torque occurs first at the hip, then at the knee, and lastly at the ankle. The rise of torque in the knee and ankle occur during that part of the launch when the heel is in contact with the ground and are consistent with onset of VL and MG activity (Fig. 2). In contrast the rise of torque in the hip occurs earlier, a time coincident with the latter part of the preparatory phase. This earlier rise in

hip torque is consistent with the observation that ST activity starts in the preparatory phase.

In terminal experiments, maximum isometric torques were obtained from two animals for comparison with torques developed previously by the same cats jumping vertically. For these terminal measurements, one hindlimb from each cat was placed in positions corresponding with those occurring in the jump. For a limb position corresponding to that which occurs during the preparatory phase, the isometric extensor torque obtained in the acute experiment was much greater than the torque occurring during jumping (Fig. 5 C, D, E). Such a difference is expected since, during jumping, hindlimb extensor muscles producing these torques are either inactive or becoming active. For a position corresponding to one in the launching phase, the isometric torques at the ankle, in contrast with those at the knee and hip, agreed well with torques generated in the jump. (Fig. 5 E, times later than that indicated by dashed line). The difference in knee torques (Fig. 5 D) probably results from the dynamic properties of muscle (see Discussion). Activation of the hamstring muscles during the jump, as evident, e.g. by ST activity, produces knee flexor torque (Fig. 5, \square), which also reduces the apparent difference in extensor torques. The difference in hip torques (Fig. 5 C) is probably due to the fact that adductor femoris is expected to be activated during the jump. However, this muscle was not stimulated in the terminal experiments.

DISCUSSION

Cats jumping to their maximum achievable heights were studied since this propulsive task was expected to invoke a maximum voluntary effort requiring synchronous kinetic activity in the hindlimbs without forelimb participation. Indeed, it was found that only the hindlimbs contribute to the cat's propulsion but their contribution is not with complete bilateral synchronization. The first part of the propulsion phase, the preparatory phase, can manifest itself kinetically in a way which does not require synchronization of both hindlimbs (e.g. Fig. 1 B). Such force asymmetries will naturally cause some lateral movement. In most jumps, however, there is bilateral symmetry in the preparatory phase (e.g. Fig. 1 A). In contrast to the asymmetry that can occur in the preparatory phase, bilaterally synchronized forces were found to occur during the launching phase in every jump studied. The whole propulsion phase of the jumping cat can thus be approximated and analysed as a planar movement involving synchronization of the hindlimb. As a result only the resultant force developed by both hindlimbs is needed for analysis.

The variability of the total vertical force trajectory during the preparatory phase and the stereotypy of the trajectory during the launching phase (Fig. 2, top) suggest that the preparatory phase is programmed to provide initial conditions for the launching phase. The net vertical impulse must be the same from maximal jump to maximal jump since the momentum at lift-off in these jumps must be equal, assuming the cat's height at lift-off is the same from jump to jump. Since the force trajectory during the launching phase is the same from jump to jump, this phase contributes the same amount to the force impulse in each jump (about 75%). The remainder of the net area under the force-time curve must also be unaltered from jump to jump. Since the force trajectory in the preparatory phase can vary from jump to jump, there is equality

Among the net vertical impulses only at the end of this phase (point B in all figures). It similarly follows that during the preparatory phase the vertical velocity of the cat's centre of mass may vary in time course from jump to jump but at the end of this phase the cat must attain the same velocity in every maximal jump. During the launching phase, the vertical velocity profile must be unaltered from jump to jump. Similar reasoning also suggests that the position of the cat may traverse a variable path during the preparatory phase but that it must follow a stereotypic path during the launching phase. Hence the position and velocity of the cat (or the 'state' of the cat) at the beginning of the launching phase is the same from maximum jump to maximum jump.

The variability evident in the preparatory phase suggests that muscular activation is variable in this phase of initialization. Since the only apparent extensor muscle group active during this phase is the hip extensor group (e.g. ST in Fig. 2), our finding that the EMG onset in ST was variable from jump to jump is consistent with the kinetic observation. Variability in kinetics and in ST activity suggest that, during this phase of the jump, neural control of muscular activation is influenced by peripheral feedback. Such feedback would guarantee that an appropriate kinematic and kinetic state be established before the launching phase begins. During the launching phase, which is only about 150 ms long, neuromuscular control might be preprogrammed ('open-loop'). Open-loop control is consistent with the observation that forces, kinematics, and EMG activity in VL and MG muscles are stereotypic.

The following results suggest that during the maximal jump proximal extensor musculature is activated prior to distal musculature. First, EMG activity occurs in ST and presumably in other hip extensor muscles before activity occurs in VL and MG muscles (Fig. 2). The inherent assumption that ST and other hamstring muscles function principally as hip extensors appears valid because the hamstrings produce little knee flexor torque, even when tetanically stimulated, in comparison with either the net knee extensor torque generated during the jump or the maximum isometric extensor torque developed by quadriceps (Fig. 5 D). Second, the rise in vertical force during the preparatory phase might be due, in large part, to this early hip extensor contraction since back musculature does not appear to contribute significantly to propulsion (Zajac & Levine, 1979). Third, maximal EMG activity appears to occur in VL before MG, though some activity in MG is apparent before VL starts its burst (Fig. 2). Fourth, this apparent sequence of muscular activation of hip, knee and ankle muscles is consistent with the development pattern of extensor torques which follows also a hip, knee and ankle sequence (Fig. 5). Fifth, kinematics show a progression of proximal to distal movements as evidenced by rotation of the thigh before the foot (Fig. 4).

It should be noted that a proximal to distal extensor activation pattern is at variance with the more-or-less co-activated pattern believed to exist during locomotion (Grillner, 1975). A detailed analysis of simultaneously recorded electromyograms, especially during galloping, might reveal an activation pattern consistent with that observed in our study of jumping. It may be, however, that the neural control of hindlimb musculature occurring in locomotion is fundamentally different from that which occurs in jumping.

There is good agreement between ankle extensor torques generated after heel-off and those torques developed during maximum isometric contractions (Fig. 5 E). This

agreement suggests that ankle extensor muscles are maximally activated during the jump. However, during jumping, MG muscle undergoes an active stretch-shorten contraction (Fig. 3; also Walmsley *et al.* 1978); thus MG should develop more than isometric force (Katz, 1939; Cavagna, Dasman & Margaria, 1968; Joyce & Rack, 1969; Joyce, Rack & Westbury, 1969; Cavagna & Citterio, 1974). This enhancement in force may be offset, though, by less than tetanic firing rates and by the rise time associated with force development to its maximum value. In fact we found that when the ankle extensor muscle group is stimulated at 100 pps, the time for isometric force to rise to 80% peak is about 100 ms. Finally, our interpretation that the ankle extensor group is maximally activated during the vertical jump is consistent with previous results which show that about equal to or greater than isometric force is developed in the MG tendon during the jump (Walmsley *et al.* 1978), that much EMG activity occurs in medial (Walmsley *et al.* 1978) and lateral (Smith *et al.* 1977) gastrocnemius during jumping by cats onto high tables, and that computed stresses up to about 300 kN/m² (Alexander & Vernon, 1975) occur in leg muscles of dogs (Alexander, 1974), kangaroos (Alexander & Vernon, 1975) and probably humans (Alexander & Vernon, 1975) during strenuous jumps.

The extensor muscles of the hip generate much more torque in the jump than that developed by the isometric hamstring muscles (Fig. 5C). The actual discrepancy is probably even larger than that indicated in Fig. 5C, since in the jump hamstring muscles shorten during activation (e.g. ST, Fig. 3); thus less than isometric force ought to be generated (Fenn & Marsh, 1935; Hill, 1938). Some or all of this difference may be due to the contribution of adductor femoris contractions to hip extensor torque, especially since this muscle was not stimulated in our isometric experiments but appears to be active during propulsion in the dog (Tokuriki, 1979) and in the cat (unpublished observations).

The quadriceps muscle group generates much more force isometrically than that exerted in jumping after heel-off (Fig. 5D), though this reduction in force during the jump is probably due to the force-velocity property of muscle (Fenn & Marsh, 1935; Hill, 1938) rather than to less than full muscular activation. After heel-off, VL undergoes a very rapid active shortening (up to 2.8 L_0 /s) without any previous lengthening contraction (Fig. 3). These rates of shortening approach the maximum velocity of shortening of cat quadriceps muscle under 'no-load' conditions (Fenn & Marsh, 1935). In addition to the dynamic properties of muscle, less than full activation of the double-joint rectus femoris and sartorius muscles (these muscles flex the hip as well as extend the knee) might contribute to our observed difference. Of course, activation of the hamstring muscles produces knee flexor torque (Fig. 5, □) which will also reduce the net extensor torque during the jump.

It is therefore suggested that during jumping by cats to their maximum achievable heights, the nervous system commands full activation of ankle, knee and hip extensor muscles. Maximal activation of these muscles is consistent with our observation that MG, VL and ST muscles generate very little EMG activity during walking in comparison with the EMG activity from the same muscles during jumping. In contrast to maximal activation of extensor muscles single joint flexor muscles should, theoretically, be inactivated (Zajac & Levine, 1979). However flexor activity is apparent during dog jumping (Tokuriki, 1979) and is evident during cat jumping by our recordings of ED

■tivity (Fig. 2), though such activity is quite variable from jump to jump. This large variability might be due to EDL's function as a dorsiflexor of the toes, operating to regulate the grip of the force platform, rather than to its function as an ankle flexor. Even if EDL should be maximally activated during the jump, the resulting ankle flexor torque would hardly be expected to hinder propulsion. This expectation is based on the fact that maximal activation of all ankle flexor muscles produces much less isometric torque than that developed by maximally activated ankle extensor muscles (Fig. 5 E, compare open circles with crosses). It may be that in jumping and in other behaviours that demand fully activated muscles, the timing of extensor contractions might be the most essential control parameter for optimal performance (Zajac & Levine, 1979).

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