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ACTIVATION PATTERNS AND LENGTH CHANGES IN HINDLIMB MUSCLES OF THE BULLFROG *RANA CATESBEIANA* DURING JUMPING

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Summary

We measured the electromyographic (EMG) activity of seven hindlimb muscles during jumping in the bullfrog *Rana catesbeiana*. The semimembranosus, gracilis major, gluteus magnus, adductor magnus, cruralis and plantaris longus were consistently active approximately 20–40 ms before any perceptible movement, as indicated by simultaneous video recordings. Activity ended before full extension of the hindlimb and take-off. Activity in the semitendinosus was variable among the jumps recorded. Simultaneous measurements of EMG activity and length changes (*via* sonomicrometry) in the semimembranosus (SM) and gluteus magnus (GM) muscles indicated that the performance characteristics of these two muscles differed. The SM muscle (a hip extensor) shortens and is activated in a manner consistent with its producing power during a significant fraction of the take-off phase. It shortened by a mean of 26.2 % of the resting length during the propulsive phase of the two longest jumps for each frog. The delay between the onset of EMG activity and the beginning of shortening averaged 24 ms, which was brief compared with that found for the GM. The total strain and mean shortening velocity of the SM increased with jumping distance. Contrary to our initial expectations, the GM muscle does not shorten as one would expect of a muscle involved in powering the jump throughout take-off. This muscle has an extensor action at the knee, but also has a flexor action at the hip. A long delay existed between the onset of EMG activity and the beginning of shortening (46–116 ms among the individuals tested). Shortening during take-off by the GM (a mean of 16.7 % for all jumps) was much less than by the SM, and in many jumps most of this shortening occurred late in the take-off period. Although the GM cannot contribute directly to power output early in take-off, it may contribute to powering the jump indirectly by transferring energy from the hip extensors to the knee joint. We conclude that muscles previously assumed (on the basis of anatomical criteria) by ourselves and others to be powering the jump may show considerable diversity of function. We hypothesize that elastic energy storage is used to help power jumping, and therefore suggest that muscles in series with major tendinous elements should be targeted for further study.

Key words: *Rana catesbeiana*, bullfrog, muscle performance, electromyography, sonomicrometry, jumping.

Introduction

Locomotor performance in animals is dependent in part upon the functional characteristics of the skeletal muscles, and the mechanical properties of muscles have therefore been the subject of numerous investigations (e.g. Calow and Alexander, 1973; Josephson and Stokes, 1989; Stevens, 1988; Hoffer *et al.* 1989; Rome, 1990; Marsh *et al.* 1992; Marsh and Olson, 1994; Lutz and Rome, 1994, 1996*a*,*b*). Despite this interest, the performance of individual muscles during natural movements remains poorly studied, in large part as a result of the difficulty of measuring the relevant variables *in vivo* and of the complexity of the musculature involved. Recent attempts to improve our understanding of muscle function during natural movements have emphasized the use of simple locomotor systems (Marsh *et al.* 1992) or improved *in vivo* recording techniques (Biewener *et al.* 1992; Roberts *et al.* 1997). In the present study, we apply one of these improved techniques to the study of muscle function during jumping in frogs.

Frog jumping is an explosive movement from a crouched, stationary position. Jumping distance is proportional to the total work done during take-off (Marsh, 1994). Maximizing jumping distance requires maximizing the work done during take-off, which in turn requires maximizing the mechanical power output. The greater the work done during take-off, the shorter is the take-off period, and thus the greater is the power output (work/time) (Marsh, 1994; Peplowski and Marsh, 1997). The joints of the hindlimbs extend throughout the relatively brief take-off, or contact, phase of the jump, during which all the power is produced for the jump. Power output is proportional to jumping distance to the power 1.5 (Bennet-

Clark, 1977; Marsh, 1994). Recent evidence suggests that some of this power output may result from the release of energy that has been pre-stored in elastic elements prior to the beginning of take-off (Peplowski and Marsh, 1997).

The study of jumping in frogs provides an excellent opportunity to integrate the *in vivo* and *in vitro* performance of skeletal muscle (Marsh, 1994; Lutz and Rome, 1994, 1996*a*,*b*). *In vitro* studies using isotonic or isovelocity contractions predict that, for muscles to produce maximal power, they should (1) be maximally active, (2) shorten over a range of lengths on or near the plateau of the sarcomere length–tension curve, and (3) shorten at a V/V_{max}, where V is shortening velocity and V_{max} is maximum shortening velocity, that optimizes power (Lutz and Rome, 1994, 1996*a*,*b*). Despite these clear predictions, the extent to which the *in vivo* jumping performance of frogs reflects the conditions associated with the maximal mechanical performance of the muscles determined *in vitro* remains an unresolved question. Lutz and Rome (1994, 1996*a*,*b*) have argued that the muscles of the frog hindlimb do operate in such a way as to nearly maximize power output irrespective of temperature. Using an integrative approach, they provide the best data to date on the function of a single hindlimb muscle during jumping in frogs. They used high-speed cine film and electromyography to measure the change in length and activity of the semimembranosus (SM) muscle in the frog *Rana pipiens* during jumping. Their measurements indicate that, during what they define as the 'power stroke', this muscle shortens at a constant velocity very close to that predicted to produce maximum power. Because the mass-specific power output recorded *in vitro* for the SM matched the muscle-mass-specific peak power applied to the center of mass during jumping, Lutz and Rome (1994) concluded that 'most of the extensor muscles in the frog hindlimb probably behaved similarly to the SM during jumping'.

Because of the extremely high power outputs recorded during jumping (Marsh and John-Alder, 1994; Marsh, 1994; Peplowski and Marsh, 1997), it is a reasonable prediction that most of the extensors must contribute to power output during jumping. However, it is equally likely that the individual extensors show variations in function (shortening velocity and activation patterns) associated with their placement within the limb and with the architecture of the muscle–tendon complex. For example, many of the other extensors are pinnate and in series with relatively longer tendons than the semimembranosus. Unless these tendons are unusually stiff, they will stretch considerably during the initial phase of contraction. This series elasticity is to be expected if elastic storage of energy is important in frog jumping (Marsh and John-Alder, 1994; Peplowski and Marsh, 1997). According to this hypothesis, the power applied to the center of mass during take-off is due to the combined release of stored energy and direct input from the muscles. This conclusion, together with the observation that mechanical work is the variable that must be maximized to maximize jumping distance, suggests that the optimal pattern of shortening may not be easily predictable from the force–velocity curve alone. Modeling studies (Roberts and Marsh, 1997) indicate that the optimum pattern of shortening for a muscle in series with an elastic tendon and shortening against an inertial load is complex. The present study is predicated on the assumption that understanding the function of the complex series of muscles used to power jumping in amphibians will be aided by further measurements of *in vivo* length changes and activation patterns.

In this paper, we present measurements of the changes in length and the patterns of activation of two hindlimb muscles, the semimembranosus and gluteus magnus, of the bullfrog *Rana catesbeiana* during jumping. We used sonomicrometry to determine the trajectory of length changes of the two selected muscles and electromyography (EMG) to measure the patterns of activation. Sonomicrometry, originally used by cardiac physiologists, has been used successfully by several skeletal muscle physiologists to measure muscle length (e.g. Newman *et al.* 1984; Griffiths, 1987, 1991; Hatta *et al.* 1988; Hoffer *et al.* 1989; Greer and Stein, 1989; Covell *et al.* 1991; Marsh *et al.* 1992; Leevers and Road, 1993). This technique measures the linear distance between a pair of piezoelectric crystals implanted in the muscle and provides a direct and high-resolution measurement of muscle length *in situ*. We also present the simultaneous patterns of activation of several other muscles in the hindlimb, most of which have been assumed on anatomical grounds to be involved in the jump. These additional muscles included the gracilis major, cruralis, adductor magnus, plantaris longus and the dorsal head of the semitendinosus. All these muscles except the adductor magnus are biarticular (cross more than one joint).

The semimembranosus and gluteus magnus muscles were chosen for several reasons. First, both muscles are active during jumping (Lutz and Rome, 1996*a*; present study). Second, practical considerations made these muscles easy to instrument with sonomicrometer transducers. They are relatively large, their fascicles are accessible from the surface of the limb, and the fascicles are parallel and relatively long (Dunlap, 1960; Calow and Alexander, 1973; Lieber and Brown, 1992). Third, measuring the semimembranosus allows us to compare our measurements with those of Lutz and Rome (1996*a*). Fourth, the gluteus magnus is predicted to be primarily a knee extensor during the jump, compared with the semimembranosus which primarily extends the hip. However, the precise role of these muscles is hard to predict because they are biarticular with antagonistic actions at the hip and knee joints. Shortening of the semimembranosus primarily causes extension of the hip but also a slight flexion of the knee, whereas shortening by the gluteus magnus causes extension of the knee and flexion of the hip (Dunlap, 1960; Calow and Alexander, 1973; Lieber and Brown, 1992; Lutz and Rome, 1996*a*; J. M. Olson and R. L. Marsh, unpublished observations). Because all the major joints in the hindlimb (i.e. the hip, knee and ankle) extend during take-off, the net effect of the active contraction of the muscles during this phase must, of course, be extension.

Materials and methods

Study animals

Eleven adult bullfrogs (*Rana catesbeiana*) were obtained from the Charles Sullivan Company (Nashville, TN, USA). The bullfrogs were intermediate to large in size for this species (Table 1). Bullfrogs were kept at approximately 20 °C in plastic containers measuring 38.1 cm (width) × 55.9 cm (length) × 35.6 cm (height), which were provided with clean water. Platforms in the containers allowed the frogs to emerge from the water and to seek shelter under water. Animals were fed crickets (Fluker's Cricket Farm) supplemented with vitamins and calcium powder *ad libitum* at least twice a week. They were held in captivity for up to 17 weeks (range 4–118 days). The animals remained healthy and active in captivity, and generally maintained their body mass at the level measured upon delivery to the laboratory. The change in body mass was –4.2±2.3 % (mean ± S.E.M.) of the initial mass.

Table 1. *Mass, snout–vent length, maximal jumping distance and experimental use of the bullfrogs in the study*

Animal	Mass (g)	Snout–vent length (mm)	Maximum jump length (cm)
Measurements of the patterns of activation only			
2C	404	155	71
3D	240	127	70
3E	296	136	100
3F	303	135	120
Measurements of the patterns of activation and changes in length			
3A	422	158	103.3
3C	308	145	116
4C	252	136	109.2
5A	533.8	172	105
5B	470	158	112.5
6A	522.9	162	114
6B	356	162	122.9

Implantation of EMG electrodes and sonomicrometer crystals

Each bullfrog was used in one of two sets of measurements. In one set, we used implanted electromyographic (EMG) electrodes to measure the activation of several muscles of the hindlimb during jumping. In the second set of measurements, the changes in length of the semimembranosus and/or gluteus magnus muscles were measured in addition to EMG activity in these two muscles and several others. The semimembranosus muscle originates *via* a fleshy connection on the ventro-lateral surface of the ischium and inserts *via* a short stout tendon on the medio-ventral surface of the femur and the adjacent surface of the head of the tibio-fibula. The gluteus magnus originates *via* a fleshy connection on the dorso-lateral border of the superior process of the ilium and inserts *via* a tendon on the aponeurosis of the cruralis (Dunlap, 1960).

EMG electrodes and sonomicrometer (piezoelectric) crystals were surgically implanted in the selected muscles. Frogs were weighed and anesthetized by immersion in 0.5 % 3-aminobenzoic acid ethyl ester (MS-222). Additional administrations of anesthetic were given as required throughout the surgery. When the bullfrogs no longer responded to tactile stimulation, up to eight bipolar EMG electrodes were implanted in each frog. The EMG electrodes were constructed in the 'simple double hook' design described by Loeb and Gans (1986) using 0.076 mm diameter, Teflon-coated stainless-steel wire. The two leads were stripped for approximately 0.5 mm at the ends and twisted several times to hold the tips 1.5–2 mm apart. Electrodes were implanted with the bared ends of the leads parallel to the muscle fibers. The muscles used were the semimembranosus (SM), gracilis major (Gr), dorsal head of the semitendinosus (ST), cruralis (Cr), adductor magnus (AM), gluteus magnus (GM) and plantaris longus (PL) (Fig. 1; muscle nomenclature follows that of Dunlap, 1960). The PL of frogs is often referred to as the gastrocnemius. After implantation, the free ends of the electrodes were passed subcutaneously to an exit point along the midline of the back. All EMG leads were soldered to a light-weight multi-pin connector (Microtech), which was

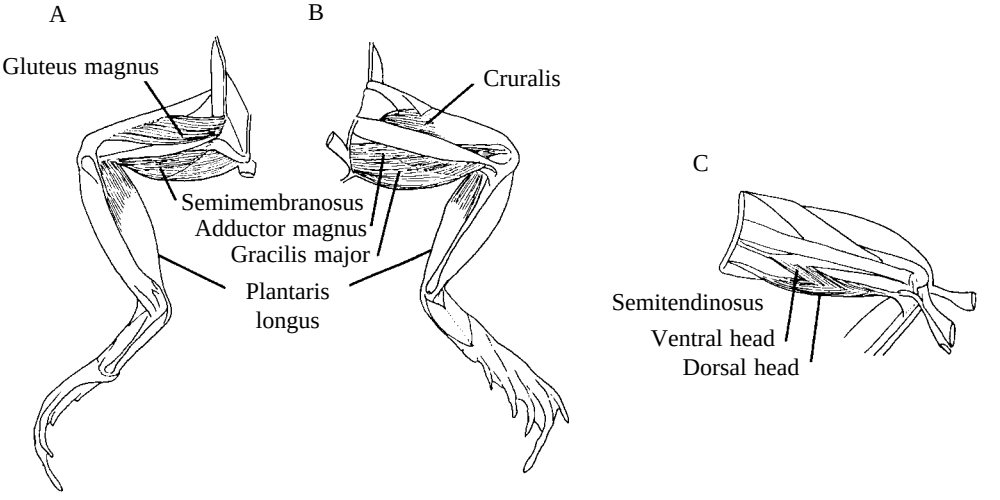

Fig. 1. Muscles of the hindlimb of the bullfrog *Rana catesbeiana* used in this study. (A) Dorsal view; (B) ventral view; (C) detail of the semitendinosus muscle. EMG electrodes were implanted in the adductor magnus, cruralis, gluteus magnus, gracilis major, plantaris longus and semimembranosus muscles and in the dorsal head of the semitendinosus muscle. Sonomicrometer crystals were implanted in the semimembranosus and gluteus magnus muscles. All but the adductor magnus muscle are biarticular (see Dunlap, 1960, for a description of origins and insertions).

subsequently sealed in epoxy resin and sutured firmly to the skin of the frog. Care was taken to standardize the location of the electrodes in all frogs; all were inserted to a depth near the middle of the muscles. The SM and Gr are divided by a tendinous inscription into proximal and distal portions; EMG recordings were from the proximal portion of these muscles. To reach the deeper dorsal head of the semitendinosus muscle, leads were passed either between the semimembranosus and iliofibularis muscles on the dorsal side of the leg or between the semimembranosus and gracilis major on the medial side.

Available evidence suggests that crosstalk among the muscles of the hindlimb did not influence our analyses of the EMGs. The specificity of the measurements was very clear when recording from the ST, which is a small muscle surrounded by much larger muscles used in jumping. There were numerous cases in which this muscle was silent while the surrounding muscles were activated. All the other hindlimb muscles of the bullfrogs are large, and the electrodes used were quite small.

To measure the length of muscle fascicles, a pair of piezoelectric crystals with a resonant frequency of 5 MHz (Triton Technology) was implanted in both the semimembranosus and gluteus magnus muscles in the left leg. We used circular 1 mm flat-plate crystals covered on one side with a hemispherical epoxy lens. In preparation for implantation, the flat side of each transducer was glued to a specially designed holder fashioned from a stainless-steel insect pin. The pin was bent to produce three orthogonal arms. One arm contained the piezoelectric crystal and was inserted into the muscle. The other two arms served as anchors on the surface of the muscle, one parallel and the other perpendicular to the long axis of the fascicles. To implant the crystal, a small incision (1.5–2 mm) was first made in the superficial fascia between two fascicles. A probe was then inserted through this incision, and the fascicles were separated to make a track along which the holder containing the crystal was inserted. Once implanted, the slit in the fascia was closed and the two superficial arms of the holder were sutured to the fascia. The second crystal was implanted 11–19 mm away from the first between the same fascicles in the muscle and oriented so that the intensity of the signal was maximized. The skin was sutured over the site and, as with the EMG electrodes, the free ends of the leads were passed subcutaneously to an exit point along the midline of the back, soldered to a multi-pin connector (Microtech Company) and sealed in epoxy resin. Care was taken to ensure that movement of the crystal was not impeded by sutures in the overlying skin. The location of the crystals in the muscles was standardized among frogs. In the SM, crystals were implanted proximal to the tendinous inscription.

Frogs were allowed at least 11 h (overnight) to recover fully from the surgery and anesthesia before being used in experiments. All frogs tolerated surgery well and recovered fully with no obvious ill effects. After full recovery from surgery, each bullfrog was weighed to the nearest 0.1 g on a Mettler top-loading balance.

Measurement protocol

Experiments were conducted over several days following surgery (typically 4 days, but up to 7 days in one animal). For the jumping experiments, individual bullfrogs were placed in a jumpway located at one end of a controlled-temperature cabinet maintained at 20 °C. The jumpway was 2 m long × 0.5 m wide and had walls 0.6 m high. Clear Plexiglas formed one of the side walls of the jumpway, providing a clear view of the jumps. The floor of the jumpway was covered with rice paper, which provided traction for the frogs. The track was marked with continuous lines at 10 cm intervals and hatchmarks at 2.5 cm intervals along the length of the jumpway. These markings were used to measure jumping distance from video recordings. Mirrors were mounted behind the frog and above the jumpway at approximately 45 ° to the horizontal to provide lateral, posterior and dorsal views of the frog throughout the jumps. Cloacal body temperature was measured using a Keithley 871 type K thermocouple thermometer at the beginning and end of the jumps on a given day. Cloacal temperature serves as a fairly accurate estimate of both overall body and muscle temperature (Lutz and Rome, 1996*a*).

All data were recorded on a Macintosh computer for analysis. For the measurements of muscle activity, the electrical output from each electrode was first amplified 1000-fold (using a WPI DAM-50, WPI DAM-6A or Grass P-15 preamplifier), with a bandpass of 300 Hz to 3 kHz. The amplified EMG signals were then digitized at 4000 Hz using a MacADIOS 12-bit A/D converter and Superscope software (GW Instruments). For the measurement of length, the output from a Triton model 120 sonomicrometer was digitized concurrently with the EMG signals at 4000 Hz using a MacADIOS A/D converter and Superscope software. The voltage output of the sonomicrometer was converted to length using individual calibrations for each set of implanted crystals. Calibrations were conducted in physiological saline with the crystals mounted on dial calipers. This calibration corrected for the ‘offset error’ resulting from the presence of the hemispherical epoxy lens and the additional epoxy resin used to mount the crystals on the holders. This correction assumes that the fixed point during the movement of the muscle is the holder which is sutured into place. A typical offset error amounted to 1.5 mm for a pair of transducers.

All jumps were video-taped at a field rate of 60 Hz with a shutter speed of 1 ms using an S-VHS video camera (Panasonic AG-160). Video recordings were synchronized with the digitized traces for muscle activity and length by a custom-designed digital-to-analog wave that controlled a light-emitting diode placed in the field of view of the camera. The control wave consisted of a 16.67 ms pulse each second followed by a series of 20 pulses each lasting 0.833 ms. One of these shorter pulses occurred in each of the following 16.67 ms intervals, but they were offset in time to sample systematically the entire ‘window’ of time during which the shutter could have been open. This method allowed us to align each field of the video with the digitized data to within 1 ms.

Sonomicrometry for measuring length changes in muscle

Because sonomicrometry is still a rather new technique in studies of skeletal muscle (Newman *et al.* 1984; Griffiths 1987; Hatta *et al.* 1988; Hoffer *et al.* 1989; Greer and Stein, 1989; Covell *et al.* 1991), it is worthwhile to review the potential advantages and pitfalls of the technique. Sonomicrometry provides the advantage of direct, relatively high-resolution, measurements of the length of the contractile portion of the muscle. It avoids errors due to the many steps and attendant assumptions necessary in transducing film data into muscle movement. This advantage is particularly important in frog jumping because the trajectory of the limb segments requires a three-dimensional analysis of the data from two views (Lutz and Rome, 1996*a*). Because the length of a fascicle segment is measured, sonomicrometry avoids the potential errors due to the compliance of tendons or other structures. However, several potential sources of error do exist. First, the transducers need to be immobilized in the muscle so that a fixed segment is measured. Our experience (see also Roberts *et al.* 1997) suggests that mounting the crystals on small holders which can be sutured to the surface of the muscle is useful in preventing unwanted movement of the crystals. The design of our holders restricts their use to muscles with fascicles running parallel to the surface of the muscle. Second, to transduce accurately the absolute distance between the crystals, the 'offset' error needs to be corrected. In our study, this potential error results from two factors. Most important is the presence of an epoxy lens on the crystal surface. Because the speed of sound is faster in the epoxy resin than in the muscle, this lens reduces the apparent distance between the crystals. Also, a small offset error is introduced by the layer of epoxy resin between the crystal and the holder, which is the element fixed in the muscle. The offset error was corrected for in this study by direct calibration of each pair of crystals (see above). The third source of error is due to the variation in the speed of sound with muscle stiffness. For frog muscle, this phenomenon is well characterized (Hatta *et al.* 1988) and could lead to a maximum error of 1.3 % as stiffness increases from its resting value to the value during a prolonged isometric tetanus. Specifically, the increase in the speed of sound could lead to an apparent shortening of 1.3 % even if the muscle remained isometric. The error in a shortening muscle would be expected to be smaller than this because the stiffness is lower (Ford *et al.* 1985). In the case of our measurements, this source of error would not influence the overall shortening measured, because muscle stimulation stops well before the minimum length is reached and stiffness should have declined considerably by this time (see Discussion). Also, the strains measured here are very large compared with this source of error. This error could lead to a slight underestimate of the muscle length in the GM during the first part of the take-off period when the muscle shortens little. Finally, the measurements in this study require the reasonable but untested assumption that the strain in the segment measured is indicative of the strain in the entire fascicle.

Data analysis

Jumping performance was assessed through analysis of the video tapes. Each jump was assigned a score on a scale of 1–4 (1 being the highest) on the basis of the quality of the jump determined through observation of the take-off, aerial and landing phases (e.g. if the frog slipped during the take-off phase or the extension of the legs was not symmetrical, the jump received a low quality score). Only jumps with a quality score of 1 or 2 were used in the subsequent analyses. Jumping distance was measured directly from the video recordings from the demarcations drawn on the floor of the track. Deviations from the perpendicular were determined by the views provided by the mirrors and were used to calculate jumping distance accurately. The durations of the take-off, aerial and landing phases of the jump were determined directly from the video recordings. Take-off was defined as the point at which the toes left the ground. The height of the center of mass at take-off when the limbs are fully extended was determined on killed frogs by fixing the frog with the limbs outstretched to a light-weight beam and determining the balance point. This point is located approximately two-thirds of the distance between the vent and the sacral joint on the back.

Electromyographic and sonomicrometric data were analyzed using Superscope software. For the EMG traces, the times of the onset and cessation of the burst of electrical activity were recorded. For the sonomicrometer traces, all traces were first offset by 20 points (5 ms) to account for the phase delay of the active filters in the Triton sonomicrometer. These filters delay the signal by 5 ms irrespective of frequency. We then recorded the time at the beginning of lengthening (if it occurred), the time at the beginning of shortening, and the time at the end of shortening. From these measurements, we calculated for each jump the amount and time course of any pre-jump lengthening, the delay between the onset of EMG activity and the beginning of shortening (t_{ES}), the total strain and the mean shortening velocity.

All data were analyzed using parametric statistics available in Systat software for the Macintosh computer (Wilkinson, 1992). Values are expressed as means ±1 S.E.M. When the effects of jumping distance were not significant for the variable of interest, we used analysis of variance (ANOVA) with Tukey *post-hoc* comparisons to evaluate the differences between means for individuals. When jumping distance significantly affected the variable, we used analysis of covariance (ANCOVA) with the dependent variable regressed on jumping distance and individual as the covariate. Statistical significance was accepted at the 0.05 level or, where appropriate, was adjusted to a lower level using the Bonferroni procedure.

Results

Jumping performance

The body temperatures of the frogs during the jumping experiments averaged 20.0±0.1 °C for the 39 days over which data were collected. The longest post-operative jumps of

individual frogs averaged 104.0±5.4 cm (range 70–122.9 cm; N=11; Table 1). This mean maximal jumping distance is similar to that reported previously for this species (e.g. Zug, 1978, 1985) during laboratory measurements at similar temperatures. Considerably longer distances have been recorded under less controlled conditions (Young, 1997). Three phases in the jump were identified from the video recordings: the take-off phase, which lasted from the first movement from the 'jump-ready' or crouched position to the point at which the frog left the substratum; the aerial phase, which lasted from this point until the frog first touched the substratum again; and the landing phase, measured as the time from the first contact with the substratum to the resumption of the 'jump-ready' position. As predicted from ballistic models, the durations of both the take-off and aerial phases of the jump were a strong function of jumping distance (Fig. 2); the duration of the take-off phase decreased with increasing jumping distance (linear regression, r^2=0.22, P<0.0001; Fig. 2A) and, not surprisingly, the duration of the aerial phase was a direct function of jumping distance (linear regression, r^2=0.67, P<0.0001; Fig. 2B). Much of the variation in aerial time is due to variation in the angle of take-off. For bullfrogs, the optimum take-off angle for maximizing jumping distance in long jumps is approximately 35 ° (Marsh, 1994); however, take-off angles of over 60 ° were occasionally observed (e.g. Fig. 2B).

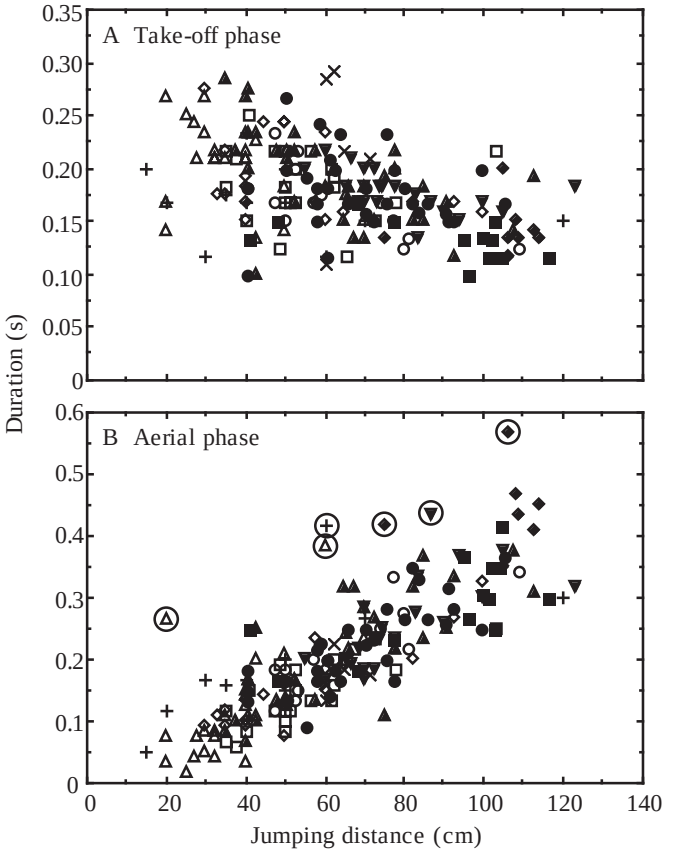

Fig. 2. The duration of the take-off (A) and aerial (B) phases of jumps as a function of jumping distance (cm) in the 11 bullfrogs used in this study. Circled data points indicate jumps which had take-off angles greater than 60 °. Key to individuals: ×, 2C; □, 3A; ■, 3C; △, 3D; ◇, 3E; +, 3F; ○, 4C; ●, 5A; ▲, 5B; ◆, 6A; ▼, 6B.

To assess accurately the work and power output during some of the longest jumps, we analyzed video recordings of the take-off and recorded take-off velocity, the take-off angle, the height of the center of mass at take-off, and the take-off duration. Work and power output during take-off were calculated using standard formulae for kinetic and potential energy at the time of take-off and take-off duration (Table 2). Take-off duration was measured from the time of the first detectable movement of the center of mass until the toes left the ground. The total mass of muscles that could be involved in the jump (see Discussion) was determined to be 18.8 % of the total body mass. For the jumps analyzed (mean jumping distance 1.05 m), the frogs expended a mean of 27.1 J kg^{-1} muscle and had a mean power output of 176 W kg^{-1} muscle. These values measured at take-off represent the total work and the mean power expended during the take-off period.

Patterns of activation of several hindlimb muscles during take-off

All the large extensor and adductor muscles in the thigh (SM, GM, AM, Cr and Gr) and lower leg (PL) were active nearly simultaneously during take-off (Fig. 3). For example, in a subsample of jumps (N=110), the lag between the onset of activity in the SM and GM muscles averaged only 4.8±1.8 ms, and the activity of the SM muscle ended only 11.9±2.8 ms before that of the GM. In almost all cases, the muscles were activated prior to any detectable movement on the video recordings and before shortening was observed in the SM and GM *via* sonomicrometry (see below). Although some variation in the duration of the EMG activity existed among animals, the activity of most muscles ceased before take-off, lasting through approximately the first one- to two-thirds of the take-off phase. The relationship between the duration of activity and jumping distance roughly paralleled that observed for the take-off phase. In the SM and GM muscles, the duration of activity decreased with increasing jumping distance (P<0.05). In the longest jumps (⩾100 cm), the mean durations of activity in the SM and GM were 111.1 and 132.2 ms, respectively.

In contrast to the case for the larger thigh muscles, the activity of the ST muscle was more variable. In some jumps, the ST was active during take-off, roughly coincident with activity in the other thigh muscles. In other jumps, even by the same frog, the ST was not active. In still other cases, the ST maintained a low level of activity throughout the entire jump.

Activation patterns and length in the semimembranosus muscle during jumping

The SM was consistently activated before the beginning of shortening (Fig. 4). The mean delay between the onset of EMG activity and the beginning of shortening (t_{ES}) of the SM ranged between 20.2 and 28.7 ms for the five frogs. Movement of the frog occurred still later than the beginning of shortening of the

Table 2. *Jumping performance, muscle work and power output of the hindlimb muscles of four frogs during three long jumps*

Frog	M_b (kg)	L_{sv} (m)	L_j (m)	Height (m)	Velocity ($m\,s^{-1}$)	t_c (s)	W_k ($J\,kg^{-1}$)	W_p ($J\,kg^{-1}$)	W_{tot} ($J\,kg^{-1}$)	W ($W\,kg^{-1}$)
5A	0.534	0.172	1.00	0.171	2.39	0.200	15.2	8.9	24.1	120.5
			1.05	0.227	2.24	0.167	13.3	11.9	25.2	150.9
			0.90	0.176	2.49	0.158	16.5	9.2	25.7	162.7
5B	0.470	0.158	1.10	0.189	2.91	0.142	22.5	9.8	32.3	227.5
			1.10	0.167	2.71	0.192	19.5	8.7	28.2	146.9
			0.90	0.200	2.50	0.117	16.6	10.4	27.0	230.8
6A	0.523	0.162	1.10	0.208	2.56	0.150	17.5	10.8	28.3	188.7
			1.10	0.216	2.35	0.133	14.7	11.3	26.0	195.5
			1.15	0.216	2.52	0.133	17.0	11.3	28.3	212.8
6B	0.356	0.162	1.05	0.197	2.61	0.158	18.1	10.3	28.4	179.7
			1.20	0.183	2.49	0.184	16.5	9.5	26.0	141.3
			1.00	0.170	2.55	0.167	17.3	8.9	26.2	156.9
Mean ± S.E.M.			1.05±0.03	0.193±0.006	2.53±0.05	0.158±0.007	17.1±0.68	10.1±0.3	27.1±0.6	176.2±10.2

M_b, body mass; L_{sv}, snout–vent length; L_j, length of jump; Height, height of jump; Velocity, velocity at take-off; t_c, contact time of jump; W_k, kinetic energy per kilogram muscle at take-off; W_p, potential energy per kilogram muscle at take-off; W_{tot}, total energy per kilogram muscle at take-off; W, mass-specific power output during take-off.

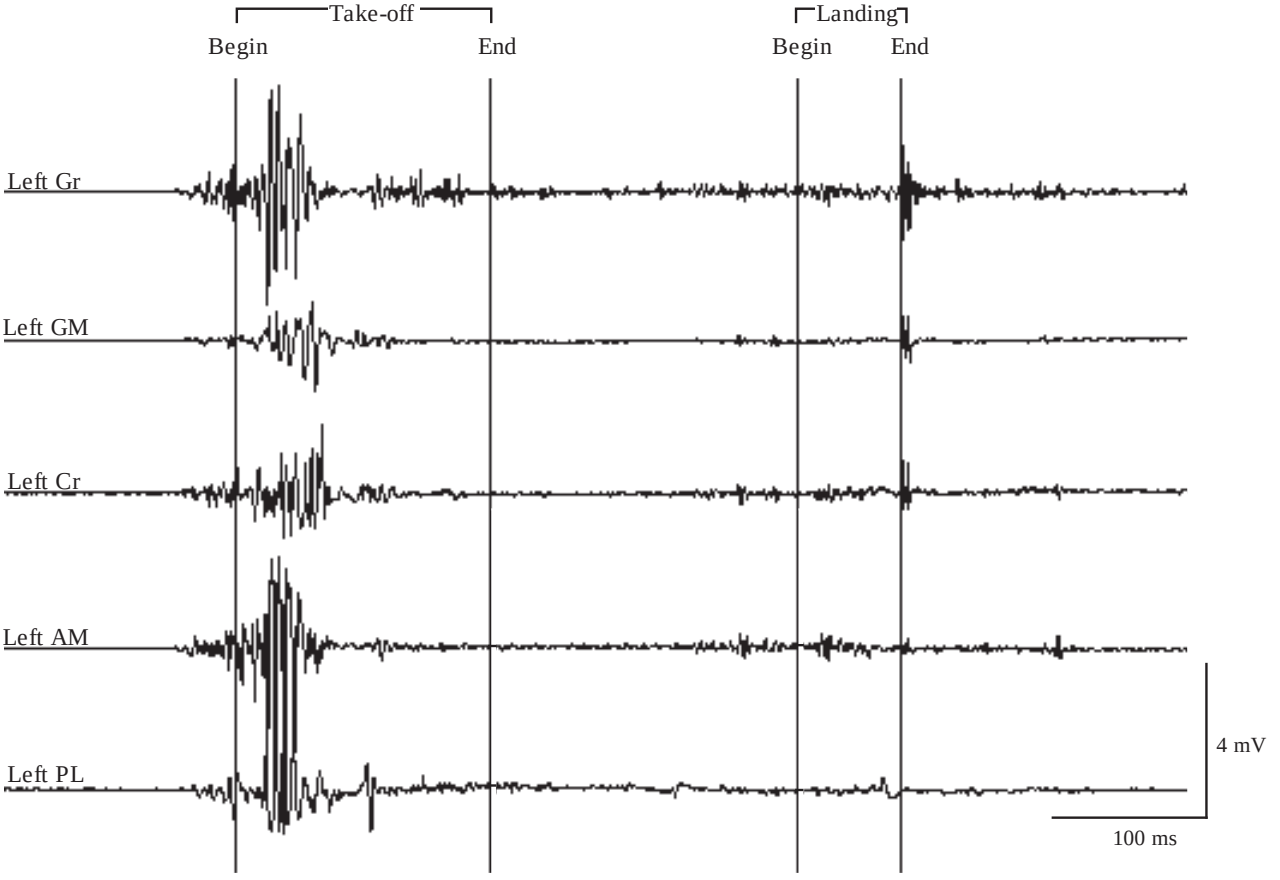

Fig. 3. Patterns of activity of several hindlimb muscles of a bullfrog during a representative jump (frog 3E; distance 82.5 cm). Each trace represents EMG data from one muscle during the jump. AM, adductor magnus; Cr, cruralis; GM, gluteus magnus; Gr, gracilis major; PL, plantaris longus.

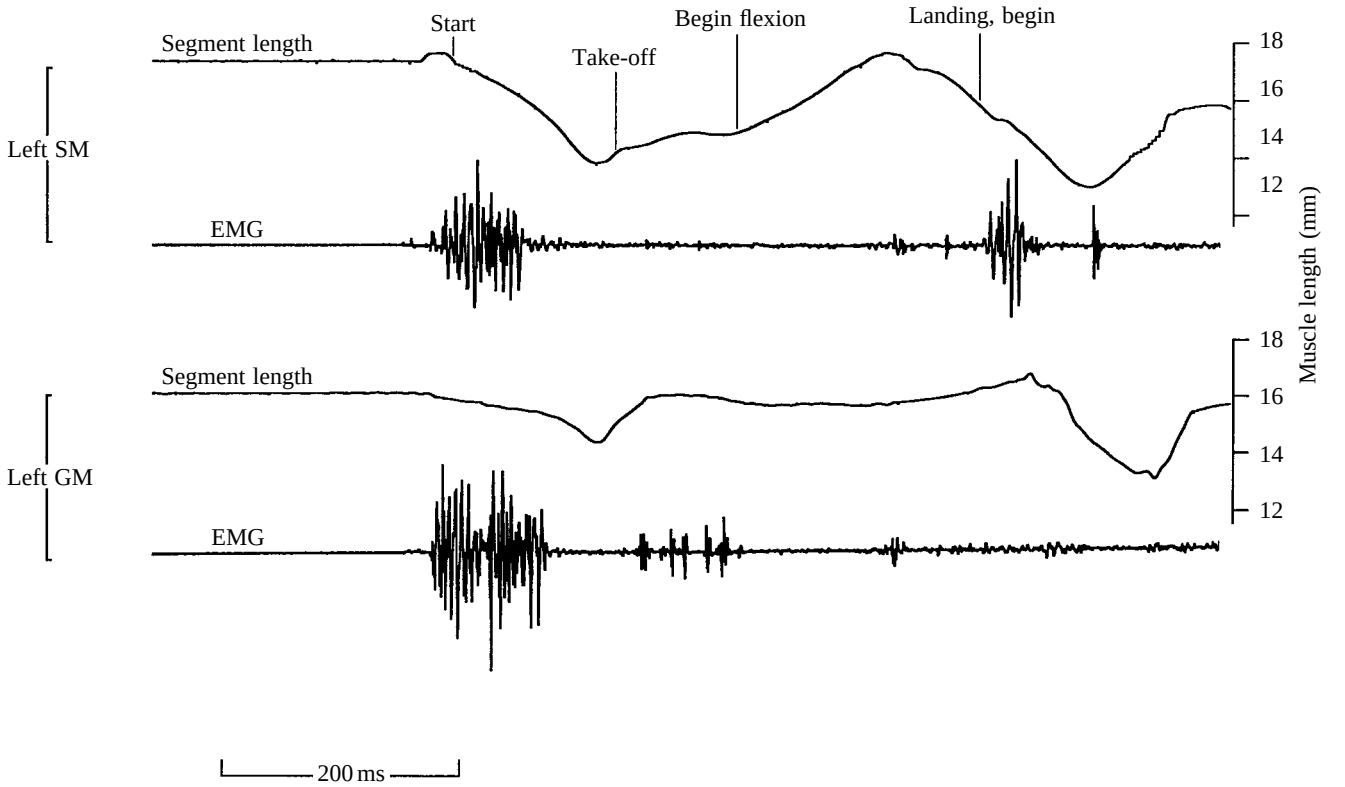

Fig. 4. Simultaneous measurements of EMG activity and length changes in the semimembranosus (SM) and gluteus maximus (GM) muscles of a bullfrog during a representative 100 cm jump. The stages in the jump as determined from the video tapes are noted on the SM trace.

SM muscle; this muscle was preactivated an average of 38.3±1.9 ms (range 158.7 ms before to 21.1 ms after; N=147) before the beginning of detectable movement on the video recordings. No differences existed among frogs (P=0.435; ANOVA) despite the differences in body size among the animals. Similarly, t_{ES} was independent of jumping distance and frog (P=0.280). The most intense electrical activity ended on average 60.7±2.5 ms (N=129) before the SM was at its minimum length. Therefore, the activity ended well before take-off as determined from the video recordings, which typically occurred after the muscle had reached its minimum length.

Fig. 5 depicts the length changes in the SM during the take-off phase of representative short-, medium- and long-distance jumps for two frogs. In general, for an individual frog, the overall pattern of length changes in the SM muscle during shortening was quite uniform among jumps over a wide range of jumping distances. In contrast, the length traces were much more variable during the aerial phase and especially so during the landing phase, owing to the concomitant variation among jumps in the timing of the flexion of the joints of the hindlimb during these two phases. Because this variation occurred after take-off, it did not affect the dynamics of the propulsive phase of the jump.

The total strain of the SM, defined as the total amount of shortening during the contraction (expressed as a percentage of resting, or pre-jump, length, i.e. the length in the 'jump-ready' position), including any lengthening before the shortening phase (see below), ranged between 20.6 and 31.9 % (mean 26.2 %) for the two longest jumps for each frog (N=6 frogs). In general, the total strain of the SM increased linearly with jumping distance (linear regression, r^2=0.23, P<0.0001; N=91; Fig. 6A). The relationship between jumping distance and percentage total strain was significant for most individual frogs; however, considerable variation existed among frogs in the slope of the relationship (Fig. 6A; P<0.001; ANCOVA).

As expected, the duration of shortening decreased with increasing jumping distance (P<0.0005). As a result, the mean shortening velocities of the SM calculated over the entire shortening phase of the jump increased linearly with jumping distance (Fig. 6B; linear regression, r^2=0.46; P<0.0001; N=87). Mean shortening velocities for jumps greater than approximately 80–90 cm ranged between approximately 1.3 and 2.0 $L_i\,s^{-1}$, where L_i is resting length, approximately double that at the shortest jumping distances measured here. The instantaneous shortening velocity of the SM during most jumps was not constant. Although the shape of the length trajectory was somewhat variable, a common pattern was for velocity to increase throughout most of the shortening period (Figs 5, 7).

In 51.1 % of the jumps (N=131), the SM muscle lengthened slightly before shortening during the propulsive phase of the take-off (see Fig. 4 for an example). In this subset of jumps, the lengthening had a mean value of 1.23±0.12 % of resting length (range 0.17–4.99 %). Neither the existence of pre-jump lengthening nor its magnitude when it did occur was

predictable from the length of the jump or the identity of the frog (P=0.913; ANCOVA). Interestingly, the muscle began to lengthen at approximately the same time as, and in many cases before, the onset of electrical activity in the muscle (8±4 ms before; N=69).

Activation patterns and length in the gluteus magnus muscle during jumping

The length trajectory of the GM muscle during the propulsive take-off phase of the jump varied greatly both within and among individual frogs (Fig. 8), although certain consistent features can be summarized. The GM muscle was activated well before it began to shorten. The mean t_{ES} of the GM muscle ranged between 45.9 and 115.9 ms among the frogs used (Fig. 9). These values were much longer than those found for the SM. The t_{ES} of the GM in one frog (6B) differed significantly from that of the others (P<0.0001; ANOVA); the mean delay of this frog (115.9 ms) was significantly greater

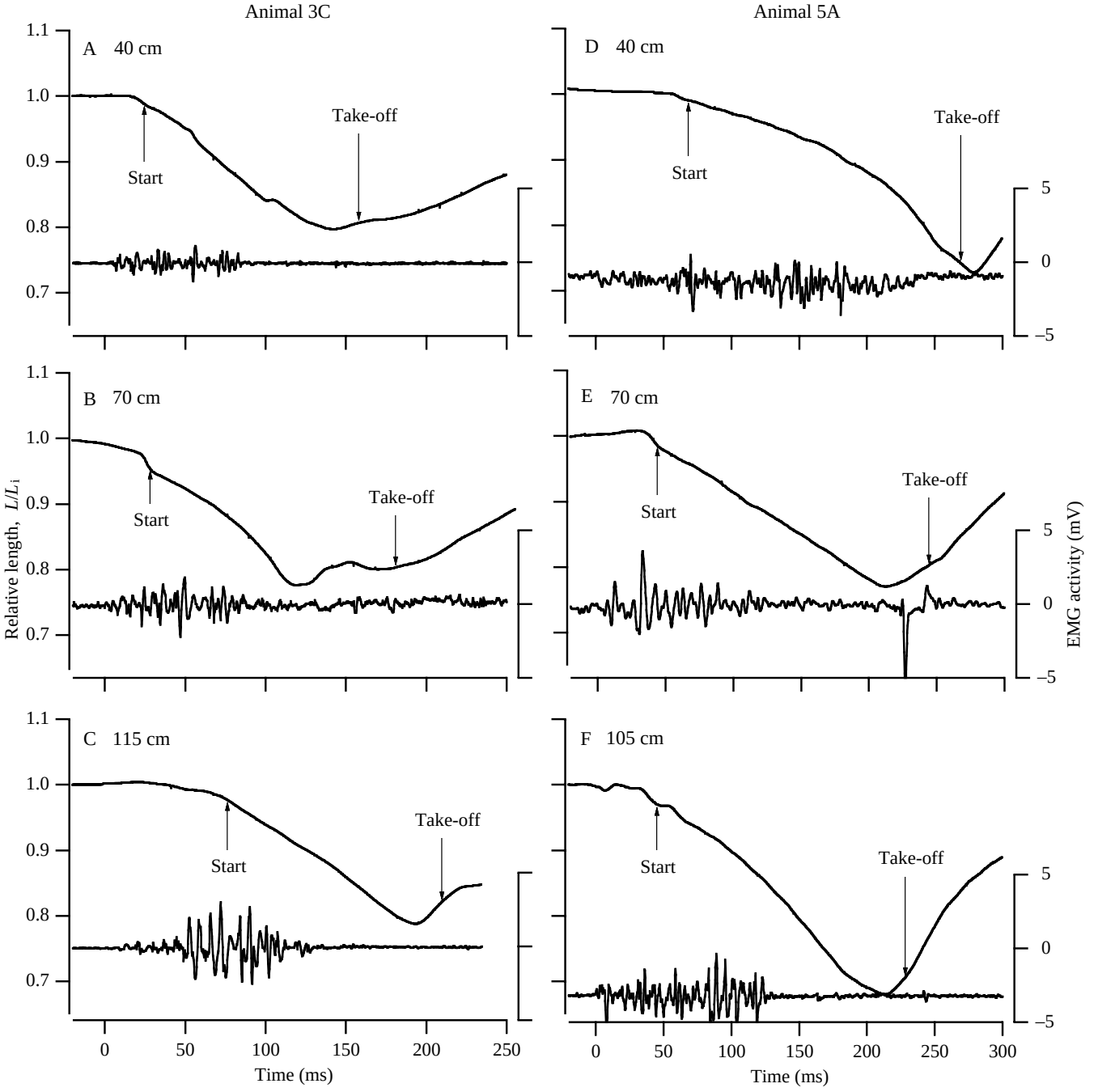

Fig. 5. Length changes and EMG activity recorded simultaneously in the semimembranosus (SM) muscle of two different bullfrogs during the take-off phase of representative short (A,D), medium (B,E) and long (C,F) jumps. Length (L) is expressed relative to the initial (resting) length (L_i).

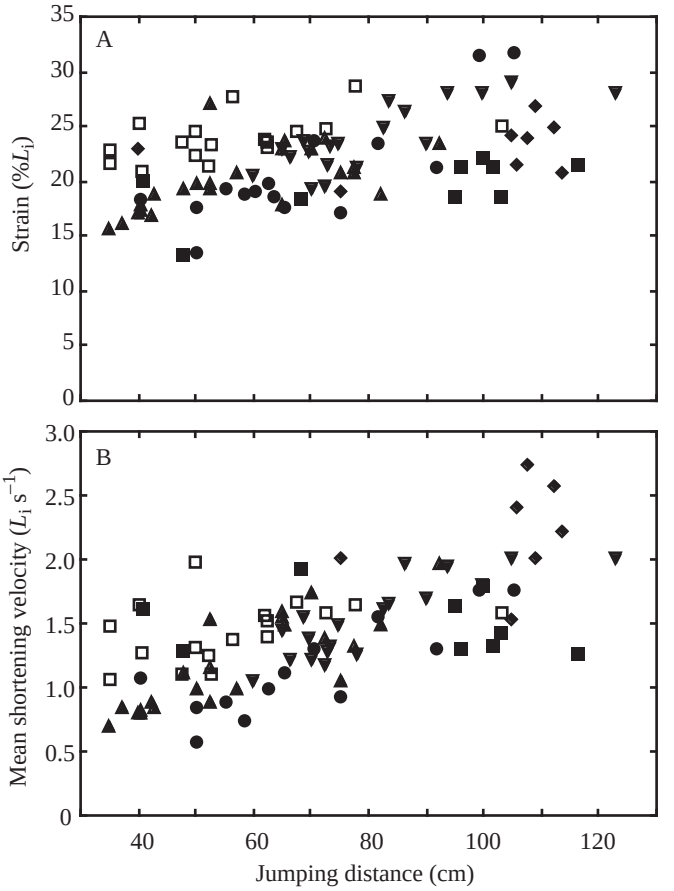

Fig. 6. Total strain (A) and mean shortening velocity (B) in the semimembranosus (SM) muscle in the bullfrog as a function of jumping distance. Strain is expressed as a percentage of initial resting length (L_i), and shortening velocities as resting lengths per second. Key to individuals: □, 3A; ■, 3C; ○, 4C; ●, 5A; ▲, 5B; ◆, 6A; ▼, 6B.

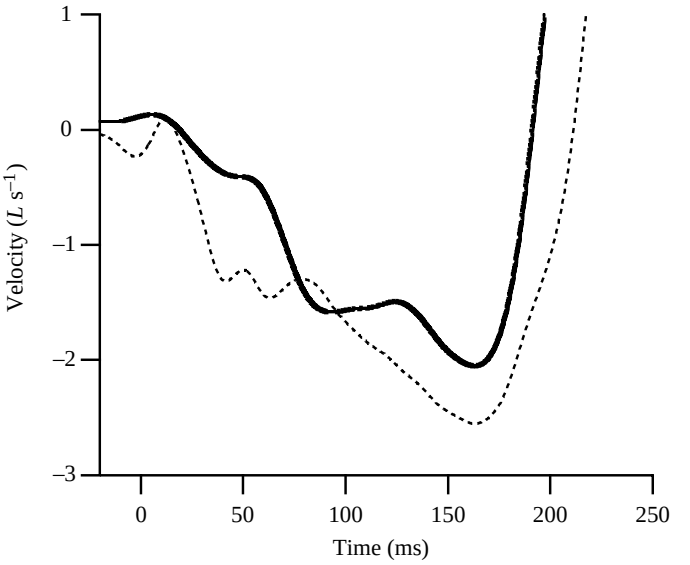

Fig. 7. Instantaneous velocity of the semimembranosus (SM) muscle during the two longest jumps for individuals 3C and 5A depicted in Fig. 6. Data from the 116 cm jump of animal 3C are shown as a solid line, and data from the 105 cm jump of animal 5A are shown as a dashed line. *L*, muscle length.

(⩾66.8 %) than that of any other frog (P<0.0002; Tukey *post-hoc* comparisons of means). The t_{ES} of the GM was independent of jumping distance for all frogs (P=0.203; ANCOVA). As for the SM, the most intense electrical activity ended a mean of 66.4±3.5 ms (N=107) before the GM reached its minimum length (Fig. 8). The total strain in the GM ranged between 9.7 and 26.1 % (mean 16.7 %) of the resting length for the two longest jumps for each frog (N=6 frogs; Fig. 10A). In general, strain in the GM was lower than strain in the SM. In contrast with the SM, the total strain in the GM was not significantly correlated with jumping distance (P=0.27; N=86).

The shortening velocity of the GM averaged over the entire shortening period increased only slightly with jumping distance (linear regression, r^2=0.08, P<0.01; N=83; Fig. 10B) and was generally lower than that for the SM (compare Figs 6 and 10). In the GM, mean shortening velocity appeared to reach a plateau of approximately 1.2 L_i s^{-1} at jumping distances greater than approximately 80–90 cm. The instantaneous shortening velocity of the GM changed throughout most of the shortening phase, usually accelerating significantly during shortening (Fig. 8).

In 79 % of the jumps analyzed (N=107), the GM muscle lengthened slightly before shortening began. In this subset of jumps, the lengthening had a mean value of 2.52±0.21 % of resting length (range 0.23–8.49 %). The extent of lengthening in one frog (6B) was significantly greater than that in most of the other frogs (P<0.001; ANOVA) and correlates with the long t_{ES} in this frog. As for the SM, however, neither the presence nor the extent of the pre-jump lengthening was predictable from the length of the jump or the identity of the frog (P=0.061; ANCOVA). The timing of the pre-jump lengthening relative to the onset of electrical activity in the GM was more variable than that in the SM, but again lengthening usually began at approximately the same time as the onset of electrical activity in the muscle (5±3 ms after the onset of EMG activity; N=84). The maximum delay between the onset of EMG activity and the beginning of lengthening in the GM was 69 ms.

Discussion

Jumping performance

The bullfrogs used in this study jumped up to 1.2 m at a body temperature of 20 °C. The longer jumps we recorded are close to the longest jumps recorded by other investigators under laboratory conditions (e.g. 1.3 m; Zug, 1978). Under the less controlled conditions of a well-known frog-jumping contest, this species has been recorded to jump more than 2 m (Young, 1997). The performance in the best jumps recorded here yielded mean estimates of muscle work and power output of 27 J kg^{-1} and 176 W kg^{-1}, respectively (Table 2). The highest

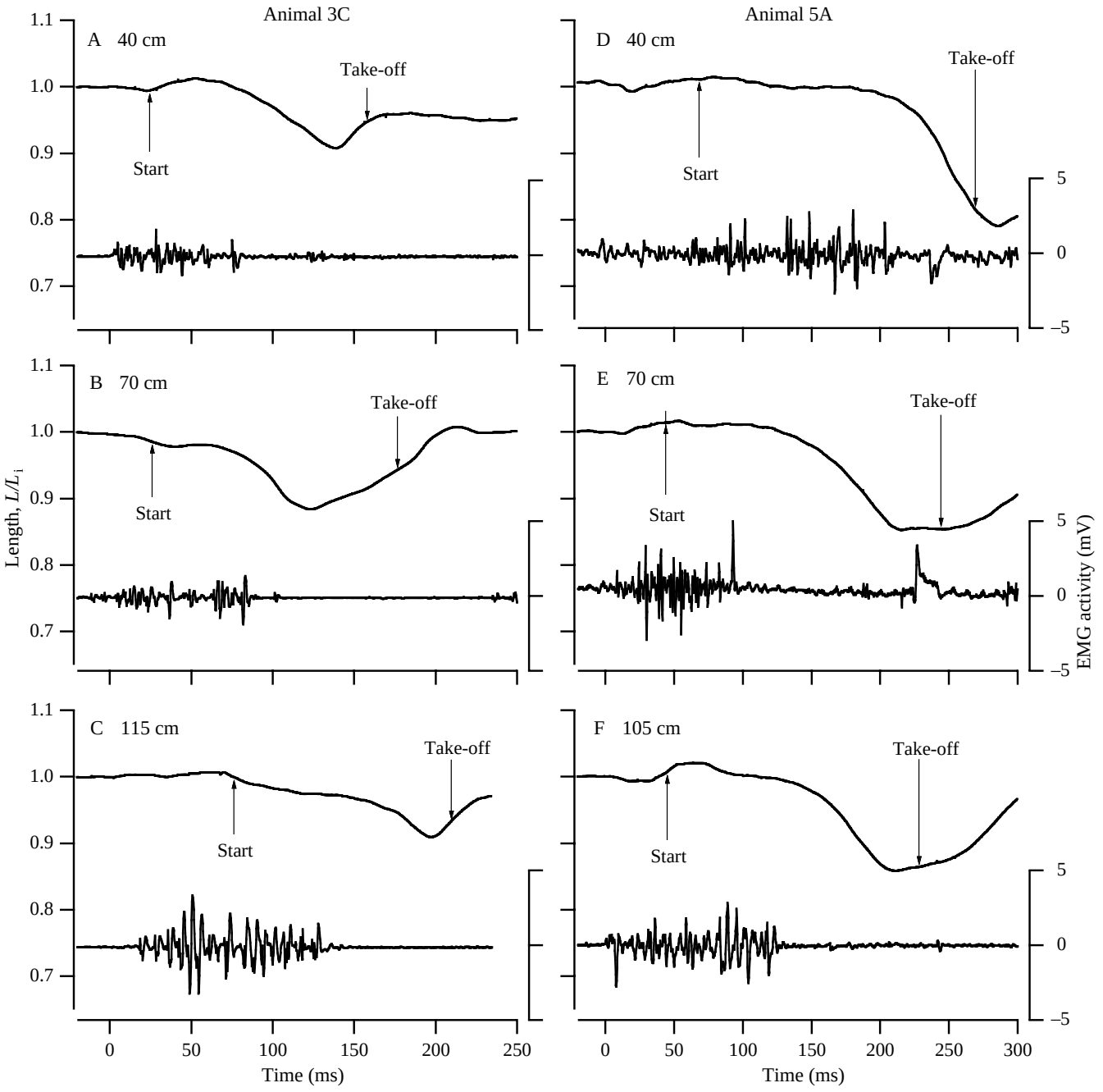

Fig. 8. Length changes and EMG activity recorded simultaneously in the gluteus maximus (GM) muscle of two bullfrogs during the take-off phase of representative short (A,D), medium (B,E) and long (C,F) jumps. Length is expressed relative to initial (resting) length (L_i).

estimates for individual jumps were 32 J kg^{-1} and 231 W kg^{-1}. These estimates of power output represent the power averaged for the entire take-off period. Assuming constant acceleration, peak instantaneous power is expected on the basis of theoretical calculations (Bennet-Clark, 1977) to be twice the mean power. In reality, acceleration is not uniform, and published measurements based on high-speed cine film of other species of frogs (Marsh and John-Alder, 1994; Lutz and Rome, 1996*a*) indicate that peak power is more than twice the mean power. Measurements of the take-off kinematics of bullfrogs using high-speed video recordings confirm a similar relationship between peak and mean power (T. J. Roberts and R. L. Marsh, unpublished results). If we assume that peak power is just twice the mean power, then power outputs for the longest jumps measured here are approximately 350–460 W kg^{-1}. The sartorius muscles of bullfrogs of the size used in this study have a maximum velocity of shortening (V_{max}) of approximately 6 L_i s^{-1}, where L_i is resting length, and a peak isotonic power of 175 W kg^{-1} at 20 °C (Marsh, 1994; R. L. Marsh, unpublished results). The semimembranosus muscle

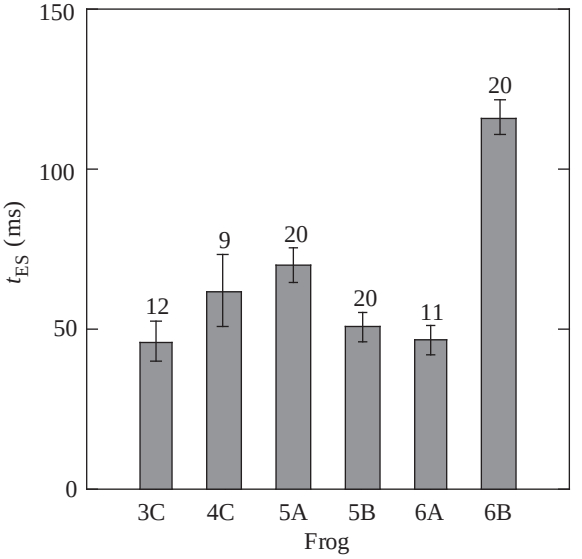

Fig. 9. Delay between the onset of EMG activity and the beginning of shortening (t_{ES}) in the gluteus maximus (GM) muscle of six frogs. Values are means ±1 S.E.M. The number above each column indicates the number of jumps analyzed.

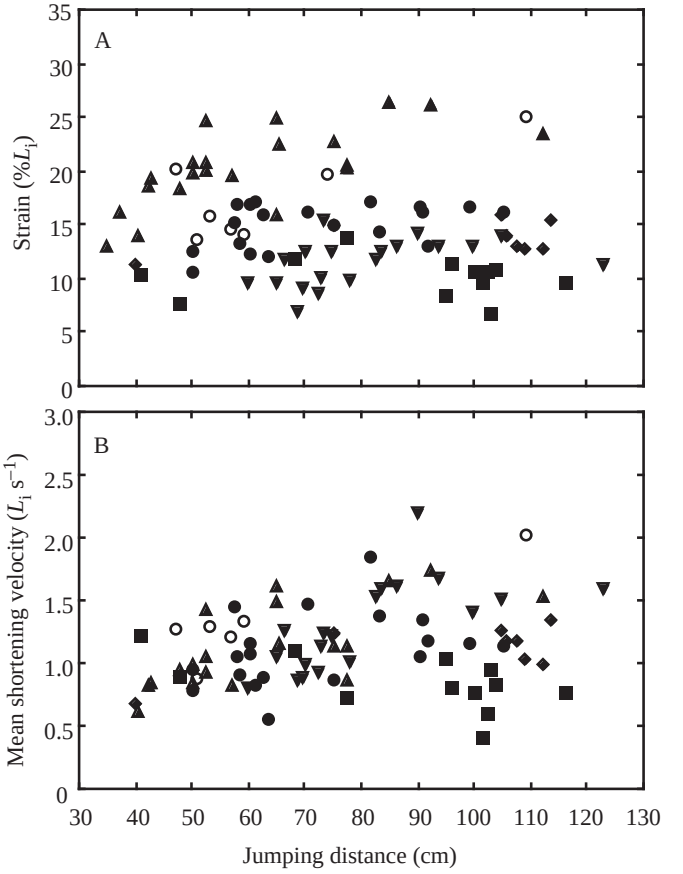

Fig. 10. Total strain (A) and mean shortening velocity (B) in the gluteus maximus (GM) muscle of the bullfrog as a function of jumping distance. Strain is expressed as a percentage of initial resting length (L_i), and shortening velocity as resting lengths per second. Key to individuals: □, 3A; ■, 3C; ○, 4C; ●, 5A; ▲, 5B; ◆, 6A; ▼, 6B.

of the much smaller *Rana pipiens* measured under isovelocity conditions (Lutz and Rome, 1994, 1996*b*) has one of the highest power outputs measured in amphibian muscles, amounting to 370 W kg^{-1} at 25 °C and 200 W kg^{-1} at 15 °C. Assuming a uniform Q_{10}, the SM of *Rana pipiens* has a power output at 20 °C (the temperature used in the present study) of 270 W kg^{-1}. Clearly, even in the jumps we recorded, which may represent less than the maximum performance of this species, the peak power output during jumping exceeds that available from the muscles based on any available data on amphibian muscle. This discrepancy suggests either that the muscles of bullfrogs other than the sartorius have power outputs *in vivo* heretofore unknown in amphibian muscle or that even these relatively large frogs take advantage of elastic energy storage to redistribute temporally the work done by the muscles. Unlike Cuban treefrogs *Osteopilus septentrionalis*, which have much higher muscle-mass-specific power outputs during jumping (Peplowski and Marsh, 1997), mean power during the jump of bullfrogs (176–230 W kg^{-1}) is more reasonable in terms of muscle performance, and thus less preactivation of the muscle is required. The maximum work output we recorded (approximately 30 J kg^{-1}) is high but well within the capacities of frog hindlimb muscle (Peplowski and Marsh, 1997).

Patterns of activation of hindlimb muscles during jumping

All the major extensor and adductor muscles in the leg that were instrumented with EMG electrodes (SM, GM, AM, Cr, Gr and PL) are active during take-off. The ST muscle is not consistently active during jumping, and the role of this muscle remains unclear (see Mai and Lieber, 1990). The muscles active in the jump are recruited nearly simultaneously before any movement is detected on the video recordings. The activity of most muscles ceases well before take-off, lasting through approximately the first one- to two-thirds of the take-off phase. In longer jumps, frogs must produce larger ground reaction forces and, as a consequence, spend a shorter time on the ground (Fig. 2) (Marsh, 1994). Correspondingly, less time is available for muscle activity, and thus, not surprisingly, we found that the duration of the electrical activity of the SM and GM is inversely related to the length of the jump. Although not quantified in this study, the obvious conclusion is that the muscles are more fully recruited in the longer jumps.

The simultaneous activation of the major thigh muscles and the PL is consistent with the hypothesis that all extensor and adductor muscles are active during jumping in frogs (Hirano and Rome, 1984; Lutz and Rome, 1994, 1996*a*,*b*). The coincident activation of several muscles of the frog hindlimb clearly accounts for the explosive nature of the frog jump and suggests that these hindlimb muscles are not recruited over different joint angles, a hypothesis proposed by Lieber and Brown (1992).

Ranid frogs, including the bullfrog, have a substantial fraction of their muscle mass devoted to muscles that could potentially power the jump. The major hindlimb muscles that could, on anatomical grounds, play a role in powering the jump are the semimembranosus, gracilis major, gracilis minor, cruralis, adductor magnus, adductor longus, gluteus magnus, peroneus and plantaris longus (Fig. 1). These muscles amount to approximately 19 % of the body mass in bullfrogs (J. M. Olson and R. L. Marsh, unpublished results). In the present study, we verified the activity of all these muscles except the peroneus, the gracilis minor and the adductor longus. Of these three, the peroneus has been found to be active during jumping in the Cuban tree frog *Osteopilus septentrionalis* (R. L. Marsh and M. M. Peplowski, unpublished results). The proportion of muscle mass devoted to muscles that could power the jump is similar to that in other ranid frogs (Marsh, 1994). However, as suggested below for the GM, the muscles that are active during jumping may not be contributing equally to powering the take-off.

Length changes and activity of the SM and GM muscles during jumping

EMG activity in the SM and GM precedes any shortening in the two muscles, as recorded by sonomicrometry, and shortening in turn starts before any detectable movement of the body detected on video recordings. In contrast, the t_{ES} of the GM is longer and in many cases the take-off is well under way before significant shortening occurs in this muscle. The mean t_{ES} for the SM for each individual frog ranged between 20.2 and 28.7 ms, and those for the GM ranged between between 45.9 and 115.9 ms. The longer t_{ES} values in the GM muscle reflect a more prolonged isometric or lengthening period in the GM before the start of shortening. A reasonable hypothesis based on these observations and on our video recordings is that extension of the hip precedes that of the knee. If the knee stays flexed, then the SM, primarily a hip extensor, will shorten, but the GM, primarily a knee extensor, will remain isometric or will lengthen as a result of its flexor moment at the hip. Hip extension has been found to precede knee extension during jumping in the frogs *Rana temporaria* and *Rana pipiens* (Calow and Alexander, 1973; Lutz and Rome, 1996*a*). The large variation in the t_{ES} of the GM suggests that the relative rates of extension at the hip and the knee are variable among jumps in bullfrogs. Resolving these issues will require high-speed video or film studies. The timing of stimulation of the GM during jumping suggests that, unlike the SM, in many jumps this muscle does not produce power or work except perhaps at the end of the take-off period.

Whether the mean t_{ES} measured *in vivo* for the SM represents the optimal delay to achieve maximal power production is unknown. Power production is a strong function of the phase of activation in a variety of muscles (e.g. Josephson and Stokes, 1989; Marsh and Olson, 1994; Lutz and Rome, 1994, 1996*b*). Lutz and Rome (1996*a*) found that the t_{ES} in the SM of *Rana pipiens* was 11 ms at both 15 and 25 °C. This value is considerably shorter than the overall mean of 24 ms measured here at 20 °C in bullfrogs. This difference may be due to the larger size and concomitantly slower movements of the bullfrogs, which have more than 10 times the body mass of the *Rana pipiens* used by Lutz and Rome (1996*a*). We have no direct information on the optimal delay for power production in the muscles of bullfrogs, but in the SM of *Rana pipiens* this optimal value has been found to be approximately 18 ms (Lutz and Rome, 1994, 1996*b*).

While it is tempting to speculate on the possible significance of the lengthening that precedes the shortening of the SM and the GM during some jumps, we consider it unlikely that this active stretch is important for muscle performance during jumping. First, the lengthening of the fasicles, particularly in the SM, is quite small and does not occur consistently during the jumps, even among those in the same animal. When it does occur, the lengthening begins coincident with or shortly after the start of EMG activity, when the force development by the muscle is expected to be low. Therefore, studies that involve stretching fully active muscle fibers are not entirely relevant to this situation (Cavagna *et al.* 1968, 1985; Cavagna and Citterio 1974; Edman *et al.* 1978). Also, frogs jump without any countermovement that could use potential energy to stretch the fibers. In a standing jump, any energy used to stretch active muscle fibers must come from other muscles in the hindlimb, thus decreasing the likelihood that the stretch would significantly increase the overall work output of the hindlimb muscles. Of course, if our hypothesis concerning the use of elastic energy is correct, then the tendons must be stretched considerably during the early phase of muscle contraction.

Role of the semimembranosus muscle in jumping

The present study supports the work of Lutz and Rome (1994) suggesting that the SM is important in producing work and power during jumping. The general pattern of length change recorded here for this muscle is quite similar to that estimated by Lutz and Rome (1994, 1996*a*) on the basis of filming studies. This muscle shortens substantially during the jump, and the largest strains are greater than 30 % of the prejump length. The shortening occurs while the muscle is active, as indicated by EMG recordings (Figs 4, 5). Further, the total strain of the SM (expressed as a percentage of resting length), increases linearly with jumping distance (Fig. 6A). The increased strain suggests that the limbs are not fully extended during shorter jumps, an observation that is confirmed by the video recordings. Increased strain would be expected in longer jumps to allow for increased work output. As expected from the shorter contact times and larger strains, the mean velocity of shortening of the SM increases with jumping distance. If the V_{max} of the SM in bullfrogs is similar to that of the sartorius ($6.0\,L_i\,s^{-1}$ at 20 °C; Marsh, 1994), then shortening velocities recorded in the SM in longer jumps ($1.32–2\,L_i\,s^{-1}$) correspond to V/V_{max} values of 0.22–0.33, which are similar to those predicted to yield nearly peak power output in other species (Lutz and Rome, 1996*b*). However, predictions about performance based on mean shortening velocity during take-off are not straightforward because in

many jumps the velocity of the SM increases during the take-off (Fig. 7). The low initial velocity may allow greater force production early in the jump.

EMG activity in the SM stops approximately 61 ms before the end of shortening. The residual force at the end of shortening in this muscle will depend on the rate of deactivation of this muscle under the conditions of shortening found *in vivo*. For the bullfrog sartorius, the time from the last stimulus to 90 % relaxation is approximately 80 ms when the muscle is shortening at $0.35V/V_{max}$ (R. L. Marsh, unpublished observations). On the basis of these data, we predict that the SM will be substantially relaxed at the end of shortening. The prediction that the SM has a low residual force at the end of shortening is consistent with the observation that this muscle actually begins to lengthen again immediately after shortening is complete (Fig. 5).

Role of the gluteus magnus muscle in jumping

At the outset of this study, we assumed that the gluteus magnus would be an important muscle in powering jumping in frogs. The muscle is part of the triceps complex that provides an important extensor moment at the knee. However, our data indicate that this muscle functions quite differently from the SM. On average, the total strain in the GM is low relative to that in the SM (Fig. 10). The mean difference in strain when compared within the same jumps is 7.19±0.72 % (paired *t*-test by jump: $P<0.0001$; $N=63$). In contrast to the SM, the overall relationship between total strain in the GM and jumping distance is not statistically significant (Fig. 10A). In jumps of over 100 cm, the mean strain of the GM was only 12.7 %. When it does shorten by more than 10 %, e.g. animal 5A in Fig. 8, the shortening often occurs late in take-off. In these jumps, in which the GM does not shorten or only shortens slowly during much of take-off, it cannot be producing much work or power during this time. However, it may contribute to powering the jump indirectly by transferring energy from the hip extensors to the knee joint. This work could go into knee extension directly or be used to stretch the tendon of the GM. In the latter case, the muscle–tendon unit of the GM may produce considerable power as force declines in this muscle late in take-off and the work produced by the hip extensors is released. Whether the muscle fibers themselves can produce significant work during this phase will depend on the deactivation kinetics of the fibers. EMG activity in this muscle ends a mean of 66 ms before the end of shortening. To produce power for all this time, the GM would have to have fibers with quite slow activation kinetics compared with the fibers of the sartorius in these animals, which would be expected to reach 90 % relaxation in 80 ms during shortening (see above for the SM).

Interestingly, the GM may play more of a role in powering the initial kick that starts a swimming sequence. During these kicks, the muscle shortens further and the shortening begins shortly after the onset of EMG activity (J. M. Olson and R. L. Marsh, unpublished observations). These results suggest that some muscles in the hindlimb of ranid frogs may alter their function depending on whether the animal is jumping or swimming. Many ranid frogs, including *Rana catesbeiana*, spend considerable time in the water, and it is plausible that their hindlimb morphology may represent a compromise between specialization for terrestrial and aquatic locomotion. In this regard, it is intriguing that ranids have larger muscle masses than the more terrestrial hylids despite the fact that in many cases the hylids are superior jumpers (Zug, 1978; Peplowski and Marsh, 1997; present study). Perhaps some of the extra mass in ranids is devoted to powering swimming. Such a suggestion cannot be evaluated fully by comparing such disparate groups as ranids and hylids, but will require comparisons within more closely related species of frogs with different locomotor habits.

Conclusions

The results presented here make it clear that considerable diversity of function, as evaluated by shortening and activation patterns, occurs among the muscles used in frogs during jumping. Muscle function also changes markedly with jumping distance. Several characteristics of the jump, including the duration of activation, strain and both mean and instantaneous shortening velocities, change with jumping distance. The observed patterns of activation and shortening seen in the SM muscle of *Rana catesbeiana* during jumping agree in general with those found for the smaller *Rana pipiens* and suggest that this muscle produces power throughout most of the take-off phase. The length trajectory of the SM recorded here differs somewhat from that recorded for *Rana pipiens* by Lutz and Rome (1996*a*), and it remains to be seen what influence the variation in instantaneous velocity during the jump has on work and power output. In contrast to the SM, the operating conditions in the GM appear suboptimal for producing power and work during most of the take-off period in many jumps, and this muscle must serve some other role during this period. Further work is required to understand the basis of the impressive muscle performance in jumping frogs. If the hypothesis that elastic storage of energy is important during jumping (Marsh and John-Alder, 1994; Peplowski and Marsh, 1997, present study) is correct, then it would be well to examine the performance of muscles that are attached to substantial tendons, such as the plantaris and the cruralis.

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