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Muscle directly meets the vast power demands in agile lizards

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Level locomotion in small, agile lizards is characterized by intermittent bursts of fast running. These require very large accelerations, often reaching several times *g*. The power input required to increase kinetic energy is calculated to be as high as 214 W kg^{-1} muscle (±20 W kg^{-1} s.e.; averaged over the complete locomotor cycle) and 952 W kg^{-1} muscle (±89 W kg^{-1} s.e.; instantaneous peak power). *In vitro* muscle experiments prove that these exceptional power requirements can be met directly by the lizard's muscle fibres alone; there is no need for mechanical power amplifying mechanisms.

Keywords: power; acceleration; muscle contraction; lizard; *Acanthodactylus boskianus*

1. INTRODUCTION

In some vigorous animal movements, the power required to overcome inertial and gravitational loads can only be reached with the participation of elastic structures along with muscle. These structures function like catapults: the elastic strain energy initially stored in them through muscle action is returned at an increased rate, thus allowing mechanical power amplification. An extreme example is the use of the resilin pad by fleas to power their acceleration at 200*g* (Bennet-Clark & Lucey 1967). Also, in frogs and bush babies, tendon enhances the power delivery from the leg muscles during jumping (Marsh & John-Alder 1994; Aerts 1998).

These well-known examples all refer to extreme jumping performance, a *non-cyclic* terrestrial style of locomotion. *Cyclic* level locomotion in small, agile lizards is characterized by intermittent bursts of fast running (Huey & Hertz 1984; Irschick & Jayne 1998, 1999). The fast accelerations required for this style of locomotion might also represent extreme inertial loads for the limb muscles. An elastic enhancement, similar to that used by fleas, frogs and bush babies, might be essential for the high performance during lizard accelerations. To investigate this possibility we have estimated the power requirements (both instantaneous and average) for rapidly accelerating lizards and compared them with the measured intrinsic power output capacity of their muscles. The results show that lizard muscle is capable of meeting the power requirements for its rapid acceleration.

2. METHODS

(a) *Animals*

Acanthodactylus boskianus is a Mediterranean, insectivorous lacertid lizard living in open habitat. Nine specimens (body mass 2.5–8 g, snout-vent length 46–73 mm) were obtained from a local dealer (Antwerp, Belgium) and kept in pairs in 100×50 cm glass terrariums. Light and heat were provided by 150 W light bulbs for 10 h d^{-1}. Animals were fed live crickets dusted with vitamins. Water was always available.

(b) *Modelling and* in vivo *measurements*

Aerts *et al.* (2003) described in detail how the 'step by step whole body kinematics' (i.e. instantaneous acceleration, velocity and displacement of the centre of mass) of lizards during fast starts can be simulated on the basis of modelled ground reaction force patterns (GRF; see for instance figure 1*a*). Briefly, GRF time profiles can be calculated based on observed step cycle information (step frequency, duty factor and number of steps to maximal speed) used by the specimens to reach their final running speeds. These computations rely on the momentum–impulse equation: the gain in speed from one step to the next must equal the impulse of the fore–aft forces during that step divided by the specimen's mass. For the present simulations, propulsion was assumed to be generated throughout each period of stance during the acceleration phase of the simulated escape (figure 1*a*) as suggested by EMG-recordings from running lizards (Reilly 1995; Nelson & Jayne 2001).

Cycle frequencies and the number of steps needed to reach top speed (required input for the simulations), as well as accelerations of the snout tip, were estimated from video-recordings (REDLAKE, Motionscope HR1000; 500 Hz) of the specimens when vigorously induced to flee (maximized performance). The video recordings indicated that the duty factor was always close to 0.5; this value, optimal for acceleration, was therefore used in all the simulations.

Individual top speeds were obtained from track measurements (Bauwens *et al.* 1995). Specimens were chased five times over a running track instrumented with eight infrared ports placed at 25 cm intervals. The time of crossing was recorded for each port and the shortest time interval between two successive ports was used to calculate the animal's maximal running speed.

Instantaneous power requirements for forward acceleration of the body could be calculated from the model output as the product of the instantaneous fore–aft GRFs and the instantaneous running speed. From these power profiles, the averages over a complete limb cycle were calculated

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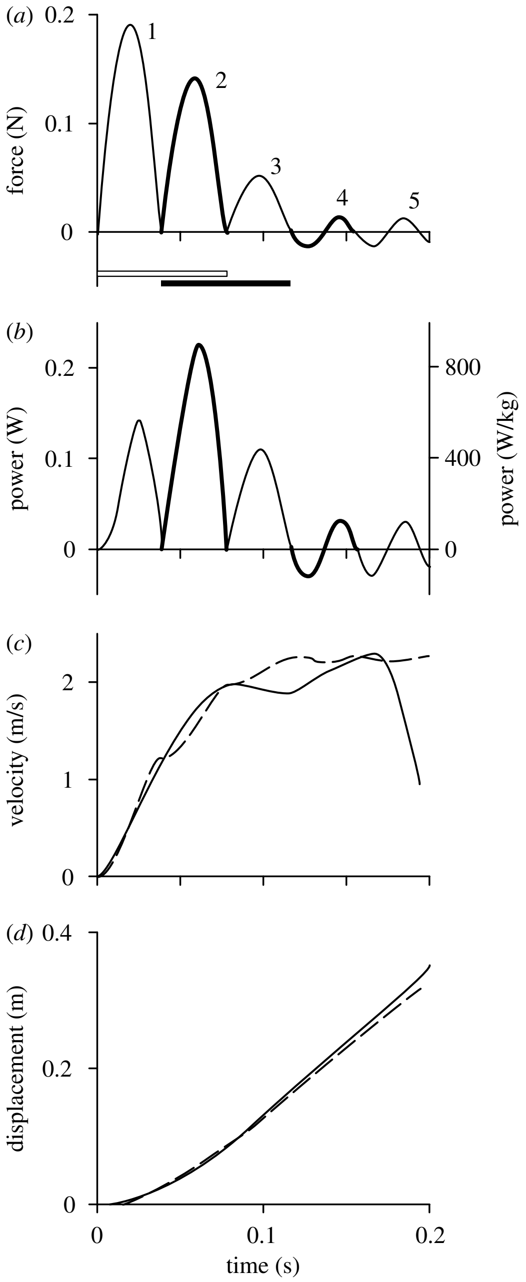

Figure 1. Power requirements in simulated acceleration. (*a*) Time-course of ground reaction force (GRF) in the fore–aft direction. Numbers refer to steps of left (thin line) and right leg (thick line). Horizontal bars mark the first strides. (*b*) Instantaneous power, product of GRF (*a*) and velocity (*c*). Right-hand scale units are power per mass of leg retractor muscle. (*c*) Comparison of simulated velocity of the centre of mass (broken line, based on force profile in *a*) with observations (continuous line) during escape response. (*d*) Corresponding displacements of centre of mass. Although the lizard did not accelerate during the third step there is a good overall match between simulation and observation.

(time integral of the instantaneous power, times the cycle frequency).

(c) *Isolated muscle*

The experiments were done on muscle fibre bundles dissected from the caudofemoralis muscle of the lizard *A. boskianus*. Fibre bundles were dissected under saline containing (mmol l^{-1}): NaCl 157, KCl 4.6, $CaCl_2$ 1.45, $MgSO_4$ 1.1, NaH_2PO_4 2.6 and $NaHCO_3$ 12.0; equilibrated with 95% oxygen and 5% carbon dioxide. A platinum foil T-clip was attached to the tendon at the femoral end of the muscle. The other end of the muscle fibre bundle remained attached to one of the caudal vertebrae, which was held in a platinum clip. Experiments were done on five fibre bundles from different lizards. Body weight ranged from 2.5 to 6.0 g. Muscle fibre bundles ranged in wet weight from 3.5 to 21 mg.

The fibre bundle was mounted between a fixed hook and a combined force transducer and motor (Cambridge Technology, Inc., Model 300-B) in a temperature controlled bath containing saline at 39 °C (±1 °C). The fibre bundle was electrically stimulated end-to-end via the platinum clips using a constant current stimulator. The stimulation and motor movement were controlled by a TestPoint program. Force, motor arm movement, and stimulus trigger pulses were recorded using a Keithley Instruments DAS-1802-AO board.

For each fibre bundle, a maximal stimulus strength and L_0, the length giving maximum isometric force, were determined.

At 3 min intervals, a series of three to six cycles of change of approximately sinusoidal length were imposed, with tetanic stimulation during part of each cycle of movement. The stimulation frequency was in the range 350–400 Hz within each tetanus. The frequency and amplitude of movement, tetanus phase and duty cycle were varied to find the conditions giving the maximum average power in the second cycle of the series. Phase is defined as time from the start of stimulation to the start of shortening expressed as a percentage of the movement cycle time. Duty cycle is defined as the duration of tetanic stimulation expressed as a percentage of the movement cycle time. In addition a ‘standard isometric tetanus’ was performed at intervals throughout each experiment to monitor progressive changes in contractile performance. The standard isometric tetanus parameters were 20 ms tetanus with stimulation at 350 Hz at L_0.

Records were made of passive force during sinusoidal movement without stimulation, and these values were subtracted from the corresponding experimental record to give the active force. The standard isometric tetanus forces were used to correct for the decline in active force, which we assumed to be caused by some fibres becoming inexcitable. Instantaneous power was calculated as the product of active force and velocity of movement. Average power in each movement cycle was calculated as the work multiplied by the movement frequency; this is equivalent to averaging the instantaneous power over the entire movement cycle.

At the end of each experiment the fibre bundle was fixed in 70% alcohol at L_0. Tendon and non-fibre materials were removed and the muscle fibre length, FL_0, was measured. The muscle fibres were dried in air and weighed (M). The cross-sectional area was calculated as

$$\mathrm{CSA} = (4.9M/d)/\mathrm{FL}_0$$

where M is the dry mass in mg, d is density (assumed to be 1 mg mm^{-3}), FL_0 is fibre length in mm, and 4.9 is the wet to dry mass ratio. The wet to dry mass ratio is derived from measurements on dogfish muscle (Curtin & Woledge 1993); similar values have been found for frog muscle (Hill 1931) and the muscles of various mice (Brooks & Faulkner 1988). Isometric force is expressed relative to CSA and power relative to wet weight to take account of differences in fibre bundle size.

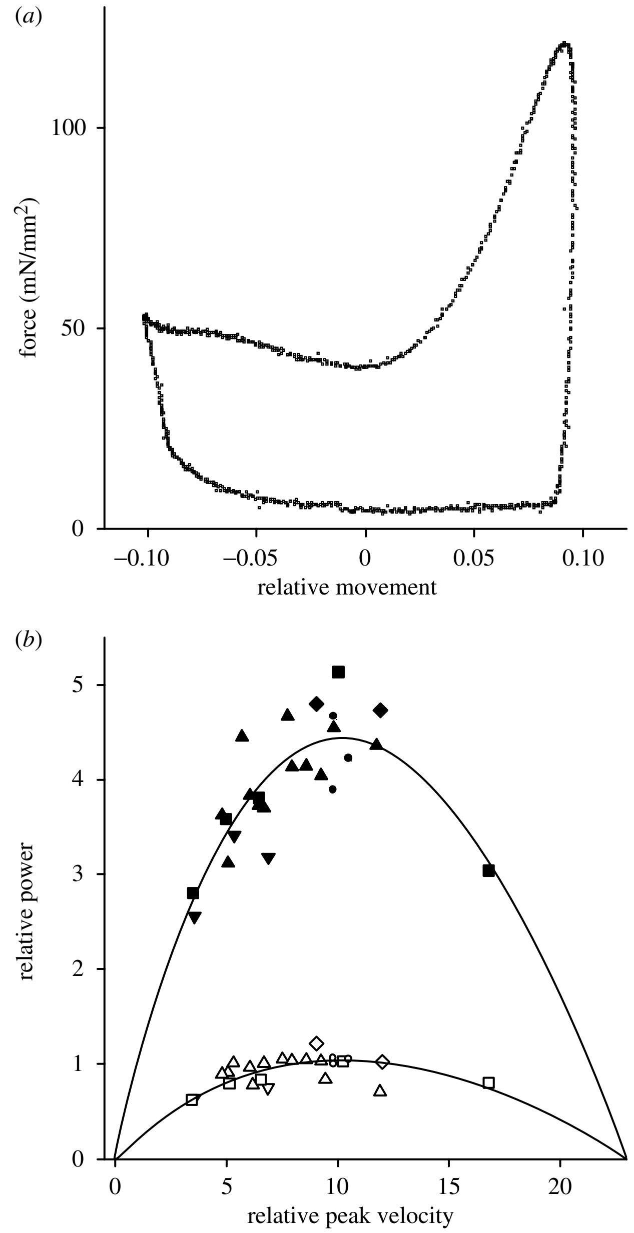

Figure 2. Power output by isolated muscle fibres. (*a*) Work-loop during sinusoidal movement, 15 Hz, stimulus duty cycle 35%, phase 10%. Force relative to cross-sectional area of muscle fibres and movement relative to FL_0. (*b*) Power output by isolated muscle from five lizards versus peak velocity during sinusoidal movement. Relative power (s^{-1}) is the ratio of power (W) to isometric force (N) and optimum fibre length (m). Relative velocity (s^{-1}) is the ratio of velocity ($m\,s^{-1}$) to optimum fibre length (m). Maximum instantaneous power, closed symbols; average cycle power, open symbols. Different symbols for different lizards. Strain cycles with amplitude 10–23% optimum fibre length at frequencies of 15 Hz. Stimulus parameters (duty cycle and phase) were optimized for cycle average power.

(i) *Statistics*

The results are expressed as means and s.e. Figure 2*b* shows the powers expressed as a relative quantity (Q, units s^{-1}), which is the ratio of power (W) to isometric force (N) and optimum fibre length (m). The value of the power (U, units $W\,kg^{-1}$, average for the five fibres bundles) was

$$U = QR$$

where Q is defined above and R (units $N\,m^{-2}$, equivalent to $J\,kg^{-1}$) is the force per CSA (average for five fibre bundles). Since Q and R each have standard error (s.e.$_Q$ and s.e.$_R$, respectively), we calculated the standard error of U in the following way:

$$\text{s.e.}_U = \sqrt{R^2\text{s.e.}_Q^2 + Q^2\text{s.e.}_R^2}$$

3. RESULTS AND DISCUSSION

Like other small insectivorous lizard species, success in both prey capture and escape from predation in *A. boskianus* depends upon rapid dashes. We have recorded several fast starts of the nine specimens during escape movements in the laboratory. Individual top speeds ranged from 1.78 to 3.57 $m\,s^{-1}$ and were reached in 0.15–0.25 s. Peak accelerations of the centre of mass up to 42 $m\,s^{-2}$ (4.3 *g*) were recorded. Stride frequencies during the accelerations varied little (11–15 Hz) and top speeds were reached in three to five steps (see also Irschick & Jayne 1998, 1999; Huey & Hertz 1984). Figure 1 shows an example of the displacement (d) and velocity (c) of the body centre of mass during an escape.

A modelling approach allowed us to estimate the power requirements, both instantaneous and the average, for each stride cycle during the observed lizard accelerations. In the second stride of the example shown in figure 1*b*, peak instantaneous power was 0.225 W and the average was 0.069 W. Forelimbs do not contribute to propulsion during these strenuous accelerations (Aerts *et al.* 2003) and often do not contact the ground. Contralateral hind limbs stride 180° out of phase and thus the maximal power requirements are delivered by the retractors and extensors of one hind limb at a time, which comprise about 6% of the body mass in this species (P. Aerts, unpublished observations). Thus, assuming that the muscles are fully activated when performing escape starts, as in the present experiments, the muscle mass specific power requirements for the acceleration phase of figure 1 are 892 $W\,kg^{-1}$ (instantaneous) and 274 $W\,kg^{-1}$ (averaged over the stride cycle). These values are much larger than those previously reported for running acceleration: 400 $W\,kg^{-1}$ (instantaneous) and 75 $W\,kg^{-1}$ (averaged over the stride cycle, assuming a duty factor of 0.5) observed in wild turkeys (Roberts & Scales 2002).

Can the high power output required by the lizard be produced by its muscles? To answer this question we used five of the nine animals mentioned above to compare the power produced by isolated muscles with the power requirement calculated above from the top speeds reached by these animals. Muscle power was measured using fibre bundles dissected from the caudofemoralis muscle, the major hind limb retractor. Power was found using the work-loop technique (Josephson 1985) during sinusoidal movements at 39 °C, similar to the animal's optimal temperature in nature (Bauwens *et al.* 1995) and to that in the performance tests. Instantaneous power was found from the product of force and velocity. Cycle average power was found by averaging the instantaneous power over the whole cycle period, not just the period of shortening. A range of strain amplitudes and cycle frequencies were used to find those giving the maximal average power during a stride cycle. The stimulus parameters (duty cycle and phase) were optimized at each strain amplitude and cycle frequency.

As shown in figure 2, power output was maximum over a range of peak velocities (product of strain amplitude and cycle frequency) between about 7.5 and 12 $FL_0\ s^{-1}$ (L_0 is the muscle fibre length giving maximum isometric force), corresponding to 16–26% strain at 15 Hz. Within this range, the power was $952 \pm 89\ W\ kg^{-1}$ instantaneous power and $214 \pm 20\ W\ kg^{-1}$ average power (mean ± s.e.; $n=5$). For these same five animals, the top speeds ranged from 1.78 to 3.33 $m\ s^{-1}$ and the power requirements for acceleration to these speeds, calculated as described above, were 940 ± 104 (mean ± s.e.) $W\ kg^{-1}$ instantaneous power and $291 \pm 33\ W\ kg^{-1}$ average power. A paired comparison of the power requirement to the muscle power showed that there was no significant difference between them ($p > 0.26$, $n=5$). Thus the power requirements for acceleration can be met by the power output from the muscles retracting and extending the hind legs.

The cycle average power output we have observed ($214 \pm 20\ W\ kg^{-1}$) from the muscles of *A. boskianus* is high compared with that observed in similar experiments on other lizards: 135 ± 7 (Johnson *et al.* 1993); and other vertebrate muscles: mouse, 49 ± 5 (Barclay 1994); mouse, 107 ± 3 (James *et al.* 1995); dogfish, 42 ± 7 (Curtin & Woledge 1996); scorpion fish, 143 ± 12 (Wakeling & Johnston 1998); quail, 83 ± 39 (Askew & Marsh 2001). We note that for the quail a much higher value is also reported that refers to the shortening part of the cycle only (Askew & Marsh 2001) and is not comparable with what we have measured. The value for the instantaneous power in *A. boskianus* ($952 \pm 89\ W\ kg^{-1}$) is very high compared with former findings (e.g. $373 \pm 16.9\ W\ kg^{-1}$ for frog semi-membranosous; Lutz & Rome 1996); however, it is not unparalleled, since a similar value, $1120 \pm 121\ W\ kg^{-1}$, has been reported for quail muscle (Askew & Marsh 2001).

4. CONCLUSION

Although in some animal movements, high acceleration demands power beyond what the muscles alone could produce, we have shown that this is not always the case. *A. boskianus* achieves high acceleration during level running with power requirements that can be met by their exceptional leg muscles.

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