

The locust jump: an integrated laboratory investigation

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Scott, Jon. The locust jump: an integrated laboratory investigation. *Adv Physiol Educ* 288: 21–26, 2005; doi:10.1152/advan.00037.2004.—The locust is well known for its ability to jump large distances to avoid predation. This class sets out a series of investigations into the mechanisms underlying the jump enabling students to bring together information from biomechanics, muscle physiology, and anatomy. The nature of the investigation allows it to be undertaken at a number of levels of complexity from relatively simple comparative observations to detailed analysis of the properties of the muscles and the energy storage systems involved in powering the jump. The relative size and robustness of the locust make it simple to handle and ideal for such investigations.

integrative laboratory class; biomechanics; muscle physiology; jumping mechanisms

MANY ANIMALS AVOID PREDATION by means of sudden, very rapid movement, elicited as part of an escape reflex. This is an important strategy for many small animals whose normal speed of locomotion is relatively slow. Different species of insect utilize a remarkable variety of mechanisms to generate an escape jump. For example, the springtails jump by means of rapid extension of the manubrium, a modified organ at the end of the abdomen (4), whereas the click beetles jump by jackknifing the joint between the pro- and mesothorax (7). Specializations of the legs associated with jumping are seen in a number of species such as fleas (3), bush crickets (6), and locusts (5).

Locusts are well known for their ability to jump considerable distances, with the jump being used by adult locusts as an escape response and to launch themselves into flight. In the undergraduate class, the large size and robustness of the locust make it an ideal model for studying the physiology and biomechanics of jumping. This series of experiments and observations is designed to allow students to investigate the jump from a number of standpoints and to bring together information from studies of anatomy, physiology, and biomechanics to explain the processes involved in jumping. As such, the study can be carried out at a number of levels depending on how much of the experimental and theoretical work is included.

The locust jump has been investigated in detail in a number of studies. As for many arthropods, the jump is dependent on the storage and subsequent rapid release of energy. In the locust, the back (metathoracic) legs show a number of specializations for optimizing jumping, including their great length (Fig. 1).

The program for the jump has been identified as comprising three stages (13). The first stage is contraction of the flexor tibiae muscle producing flexion of the femorotibial joint to

bring the tibia up against the femur. This is followed by a cocontraction phase when both the flexor and extensor tibiae muscle undergo isometric contraction. This phase lasts for 300–600 ms and allows the build up of potential energy. The jump is then triggered by the relaxation of the flexor muscles allowing rapid, powerful extension of the tibia, thus propelling the locust into the air (13). Although the flexor muscle is much smaller and weaker than the extensor muscle, it is able to maintain the leg in a flexed position because of its significant mechanical advantage when the leg is fully flexed. In part, this is due to the presence of a lump of cuticle on the inner surface of the distal end of the femur, which acts as a catch to hold the flexor apodeme (tendon) (11). When the flexor muscle relaxes, the apodeme slips off the lump, allowing extension of the leg.

This process enables the extension of the leg to occur with both the high force and high velocity needed to power the jump, overcoming the limitation that muscle cannot generate maximum force and velocity simultaneously (14). The extensor muscle is strongly pennate, with an angle of $\sim 20^\circ$ (8) and its isometric contraction allows storage of the elastic strain energy via the stretching of the extensor apodeme and deformation of the cuticular semilunar processes of the femorotibial joint (Fig. 1) (1, 6, 12). Thus elastic strain energy is stored over a period of up to 600 ms and then released as the leg extends in 25–30 ms. Heitler's website (12) provides detailed illustrations and animations of the process.

METHODS

Free jumping. Measurements of free jumping should ideally be made in a warm environment with a temperature of 25–30°C. Failing that, the locusts should be kept warm between jumps using radiant heat from a lamp.

Each locust is weighed, and the length of the femur of the metathoracic leg is measured. The wings of the locusts should be fixed together with a small strip of adhesive tape to prevent them from flying. Jumping is best effected by placing the locusts on a rough surface, such as a towel, which gives the feet purchase so that they do not slip during the jump. The students should measure the approximate jump distance and also observe the behavior of the locust during preparation for the jump. Measurement of the jumping distance may be facilitated by dipping the tarsi of the metathoracic legs of the locusts into ink.

Because the jump is an escape response, the locusts usually have to be encouraged to jump by blowing on them, pinching the abdomen, or clapping hands close to them. This stage sometimes requires patience, particularly because the response can habituate quickly. If this happens, the locust can be returned to a holding box while another one is tested. The mean data from at least five jumps should be recorded and class data for a number of locusts collected.

After the jumping measurements, one of the metathoracic legs is removed for measuring the power output of the extensor tibiae muscle (see below).

If possible, the jumping should be repeated by using 4th and 5th instars. This provides a much larger spread of data and allows more effective comparisons of the relationships between body mass or leg

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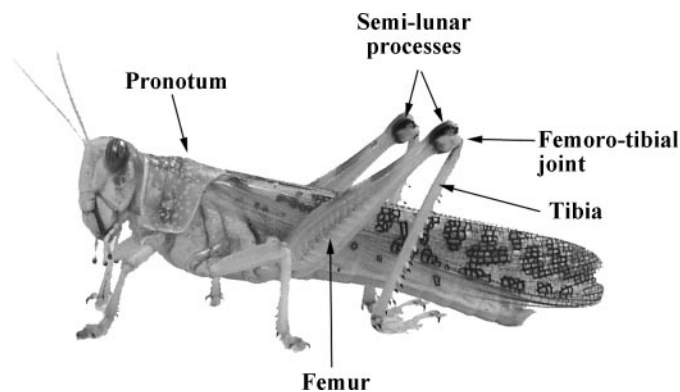


Fig. 1. Adult *Schistocerca gregaria*.

length and jump distance. It also allows discussion of the different roles jumping plays in the adults and instars (see DISCUSSION).

A number of additional experiments can be performed to test the jumping process. Four, in particular, provide results that can be discussed in detail.

The first of these is to test the effects of adding additional mass to the locust by fixing plasticene to the pronotum (Fig. 1). This loading can be measured as percent increases in body mass and can be discussed in terms of the implications for female locusts when egg bearing, which leads to a significant increase in body mass.

Second, the mechanism of the jump depends on energy storage, in great part by deformation of the semilunar processes (1) (see Fig. 1). It is possible to weaken these by gently scraping away some of the surface cuticle. This will lead to reduced jump distances. In some instances, it will result in snapping of the process when the locust tries to take off, after which the individual is unable to jump again.

Third, after molting, the exoskeleton is relatively weak and gradually hardens over several days. Again, this has significant impact on the jumping capacity, particularly for freshly molted animals (16), which tend to be unwilling to jump and, if they do jump, may suffer mechanical failure of the tibia. In species such as *Schistocerca gregaria*, the newly molted individuals are easily identifiable because the exoskeleton is pink. With ageing this gradually turns to brown and then yellow. A further option is to use a load cell to test the bending strength of the tibia in animals of different ages.

Fourth, comparisons with humans. Members of the student group can perform standing jumps and the results can be compared with those of the locust. This can also be used to extend discussion of the effects of varying joint angle for optimum power production and jumping distance.

Analysis of the jumping data. Calculations of power output are based on the analyses by Bennet-Clark (1), Heitler (12), and Hirano and Rome (15). For the purposes of a class practicum, some simplifications have been introduced and some assumptions are made. For example, it is assumed that air resistance is zero and that the locust takes off at an angle of 45° , providing an optimal trajectory. The background theory has been included here, but for the practicum class, it may well be sufficient simply to use the key equations (Eqs. A1–A4) as set out in the sample data analysis in the APPENDIX.

The locust jump is powered by the contractile forces generated by the large extensor tibiae muscles of the metathoracic legs (hindlegs). Jumping depends on the exertion of force by these legs against the ground. The active part of the jump, therefore, is only the brief period during which the legs remain in contact with the ground. For the main part of the jump, therefore, the locust is traveling through the air as a projectile.

For a projectile, the horizontal distance traveled (d) is given by the time in the air (t) multiplied by the horizontal velocity (v_h).

$$d = v_h t \quad (1)$$

The time spent traveling upwards, i.e., the time from takeoff to zero vertical velocity (v_v) is given by the vertical velocity at takeoff divided by the acceleration due to gravity (g). Therefore, the total time in the air is

$$t = 2 \frac{v_v}{g} \quad (2)$$

Substituting for t in Eq. 1

$$d = 2 \frac{v_v v_h}{g} \quad (3)$$

The vector of the velocity (v) on takeoff is the resultant of the vertical and the horizontal velocities, given by

$$v_v = v \sin \theta \text{ and } v_h = v \cos(90 - \theta)$$

where θ is the angle between the resultant and the vertical velocities.

If the effects of air resistance are ignored and the locust jumps at a takeoff angle of 45° , then the horizontal and vertical velocities are equal, i.e., $v_v = v_h$ and $\theta = 45^\circ$.

$$\sin 45 = \cos 45 = 0.707 = \frac{\sqrt{2}}{2}$$

Substituting for $\sin \theta$ and $\cos \theta$ gives

$$v_h = v_v = v \frac{\sqrt{2}}{2}$$

Substituting for v_h and v_v in Eq. 3 therefore gives

$$d = \frac{v^2}{g} \quad (4)$$

If the animal starts its jump from standing, then it has to accelerate from zero velocity to the take-off velocity. The acceleration period is restricted to the period of time the feet remain in contact with the ground and is therefore determined by the length of the legs and their degree of flexion at the start of the jump. For the locust jump, the legs are fully flexed before the jump and the extension occurs mainly as rotation of the femorotibial joint.

The acceleration distance (s) is therefore determined by the length (L) of the femur and the angle of joint rotation. The leg starts fully flexed and rotates through to an angle of $\sim 130^\circ$ at takeoff (5).

Acceleration distance (s), can therefore be calculated as the length of the arc of the circle

$$s = 2\pi L \frac{130}{360}$$

$$s = 2.27 L \quad (5)$$

Velocity at takeoff is determined by the acceleration (a) and the distance (s) over which the muscles exert that acceleration. If we assume that the initial velocity is zero (a standing jump) then

$$\frac{mv^2}{2} = mas$$

where m is the mass of the locust. The velocity is taken as $0.5 v$ to approximate to the mean velocity during the acceleration phase. This simplifies to Eq. 6

$$v^2 = 2as \quad (6)$$

To achieve this velocity, the locust has to do work over a period of time to accelerate its mass. Work per unit time is expressed as power in watts

$$P = \frac{v \cdot m}{2} \quad (7)$$

The power output in W/g of muscle can therefore be calculated from the measurements of muscle mass (see below).

Power from muscle contraction. For the measurements of muscle power, one of the metathoracic legs is removed by cutting through the coxal joint between the femur and the thorax (Fig. 1). The tarsi should also be removed. An example setup used for the recordings is illustrated in Fig. 2.

The femur is fixed in a small muscle bath using plasticene or similar fixative. The distal end of the tibia is tied to the arm of an isotonic transducer by a length of thread. If possible, this should be arranged so that the length of the lever arm from the axis of rotation of the transducer corresponds to the length of the tibia. The end of the tibia should also be tied to the edge of the bath opposite to the transducer (Fig. 2) to enable the leg to be set at the different starting angles. The transducer arm is counterbalanced by a weight that should be the same as half the mass of the locust (as measured above). This would then approximate to the loading that the leg would be working against in the intact animal and so makes for direct comparison of the power outputs under the two situations (note that changing the load will affect the power by changing the velocity of the movement. See suggested variations below). The output from the transducer is fed to a computer interface.

In our undergraduate laboratory, the system currently used for these experiments is the PowerLab computer interface system by ADInstruments operating the Scope software, with the compatible isotonic transducer. This system enables triggered stimulation and recording of the movement of the leg. The analysis software provides outputs of the peak-to-peak amplitude of the movement and the maximum

velocity of the movement in a format that can be input directly into a spreadsheet for further analysis or graphical representation.

Two thin, bare copper wires are used as stimulating electrodes. To insert these, small holes are made in the cuticle of the femur using a needle, taking care not to push the needle in too deeply, because this can cause damage to the underlying muscle. The optimum positioning is for the wires to be inserted at the midline of the lateral surface of the femur, ~5 mm apart and ~5 mm from the proximal end of the femur. The other end of the wires should be connected to a triggered stimulator. The computer recording of the transducer output can then be triggered to the stimulator output to enable timed recording of the leg movement generated by the muscle contraction.

To measure the maximum power output, the femorotibial joint angle should be set to 30° (a protractor can be used to measure the angle of the joint as shown in Fig. 2) and the leg stimulated with trains of 5 or 6 square-wave pulses of 0.5-ms duration at 20-ms interpulse intervals.

The work done by the muscle contraction is the movement of the weight against gravity, which represents the rotation of the transducer arm caused by the leg extension. The power output is the rate at which this work is done, i.e., the velocity of movement of the weight. This will vary during the muscle contraction cycle. Therefore, the maximum power output is taken from the maximum rate of movement. The power in watts can therefore be calculated as: power = max rate of movement ($m \cdot s^{-1}$) \times mass of the weight (kg) \times gravity ($m \cdot s^{-2}$). This gives the units of power as $kg \cdot m^{-2} \cdot s^{-3} = N \cdot m \cdot s^{-1} = \text{watts}$, where N is Newton.

The maximum rate of movement should be measured as the maximum slope of the movement trace recorded on the computer, calibrated for the isotonic transducer. With care, this preparation remains viable for several hours, and so the students can investigate a number of properties of the muscle contraction including, for example, the summation of contractions and the absolute and relative refractory periods by varying the number of stimulus pulses and the interpulse interval, the effects of joint angle on power output, and the effects of varying the load on the velocity of shortening and the power output.

After the experiments, the extensor tibiae muscle should be weighed. The easiest way to do this is to split the femur open by slicing off the dorsal ridge and then removing all of the muscle for weighing. This will introduce a small error, because the flexor tibiae muscle, while relatively very small, will also be weighed. However, under a dissecting microscope, it is easy to dissect away the flexor muscle so that only the extensor is weighed. Comparison can then be made of the power outputs calculated from the jumping and muscle stimulation experiments per unit mass of muscle tissue.

Internal anatomy. Careful dissection can reveal a number of anatomical features related to the jump process. At a gross level, when the femur is opened to remove the muscle, it is possible for students to observe the layout of the flexor and extensor tibiae muscles and compare their relative sizes. Furthermore, it is easy to observe the gross morphology of the extensor muscle that comprises large muscle blocks that are highly pennate. Students can discuss the biomechanical implications of such an arrangement in terms of the power output during shortening contractions and how this may relate to the jump mechanism.

More careful dissection can reveal the structure of the joint, including the lump and the layout of the muscle apodemes passing through the joint (see Ref. 12).

RESULTS

Locust Jumping

Table 1 shows a typical summary of a set of class data using adult and 5th and 4th instar *S. gregaria*. A sample set of calculations for the power output is shown in the APPENDIX. The

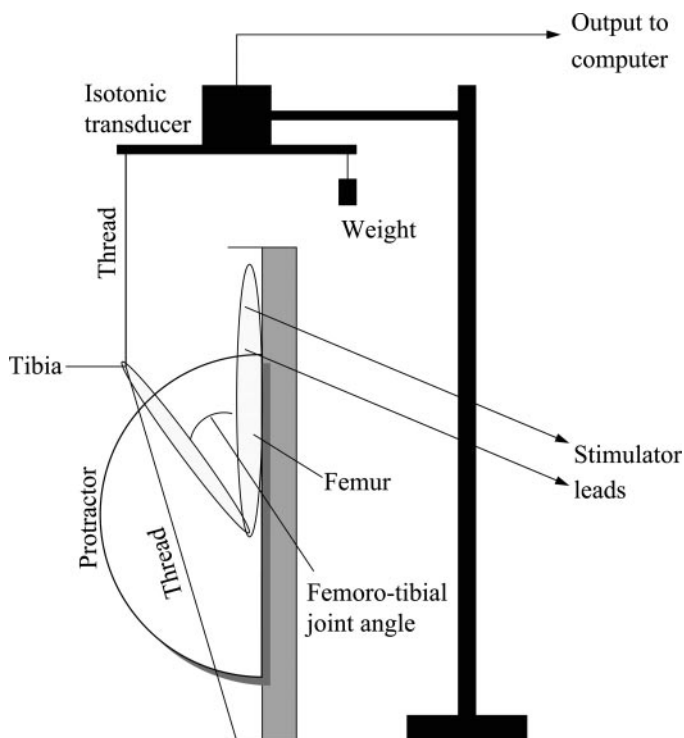


Fig. 2. Example set-up for recording the power output from the isolated leg. The starting angle between the tibia and the femur is set using the protractor.

Table 1. Summary data of the jumping outputs for adult and 5th and 4th instar juvenile *Schistocerca gregaria* locusts taken from class data

| Locust | Body Weight, g | Jump Distance, m | Femur Length, mm | Velocity, $m \cdot s^{-1}$ | Accel Distance, m | Accel, $m \cdot s^{-2}$ | Power, W | Muscle Mass, g | Power/g, W/g |
|------------|-----------------|------------------|-------------------|----------------------------|-------------------|-------------------------|-----------------|-------------------|-----------------|
| Adult | 1.60 ± 0.46 | 0.70 ± 0.19 | 20.30 ± 0.001 | 2.62 ± 0.35 | 0.05 ± 0.003 | 74.67 ± 18.82 | 0.16 ± 0.06 | 0.076 ± 0.003 | 1.05 ± 0.43 |
| 5th Instar | 0.99 ± 0.20 | 0.34 ± 0.09 | 15.50 ± 0.93 | 1.80 ± 0.25 | 0.04 ± 0.002 | 47.17 ± 13.08 | 0.05 ± 0.03 | 0.040 ± 0.001 | 0.56 ± 0.31 |
| 4th instar | 0.57 ± 0.09 | 0.26 ± 0.05 | 12.39 ± 0.99 | 1.58 ± 0.17 | 0.03 ± 0.002 | 45.08 ± 10.15 | 0.02 ± 0.01 | 0.025 ± 0.001 | 0.40 ± 0.23 |

Values are means \pm SD. No. of locusts were 24 adults, 16 5th instar, and 16 4th instar. Note that the extensor muscle mass is that for one leg and therefore has to be doubled for calculation of the power per gram of muscle.

mean jump distance for the adults was 0.7 ± 0.19 (SD) m, which corresponds to the range of 0.5 to 0.95 m reported by Bennet-Clark (1). To produce such a jump distance, the accelerations generated by the locusts are large, with the adults accelerating at a mean of $74.67 \pm 18.82 m \cdot s^{-2}$, which is ~ 7.5 times the acceleration due to gravity. This acceleration is generated by a power output of 1.05 ± 0.43 W/g of muscle, whereas the instars generated $\sim 50\%$ of this output, 0.56 ± 0.31 and 0.4 ± 0.23 W/g of muscle, for the 5th and 4th instars, respectively. These latter values are comparable to a sample class value obtained for a student athlete, which was 0.43 W/g of muscle for a standing jump.

Figure 3 illustrates a scatter plot from the class data of jump distance against body mass for the adults and juveniles. Although there is no significant correlation between body mass and jump distance within each of the three groups, taking all of the animals together indicates a linear relationship ($r^2 = 0.38$, $n = 56$). A similar relationship can be plotted for the jump distance against femur length.

Careful scraping of the lateral surface of the semilunar processes of an adult commonly gave rise to jumps that were markedly shorter than earlier jumps. In some instances, one or both processes audibly cracked during an attempted jump, after which the individuals were unable to jump again.

Measurements of the maximum power output generated by stimulation of the extensor muscle ($n = 14$) gave a value of 0.02 ± 0.02 W/g of muscle, which is significantly less than the power produced during the jump ($P < 0.01$ by Student's *t*-test).

The power output depends on the joint angle, as illustrated by Figs. 4 and 5. The maximum power output in these experiments was obtained at a femorotibial joint angle of 30° , declining to $\sim 25\%$ of maximum at 120° .

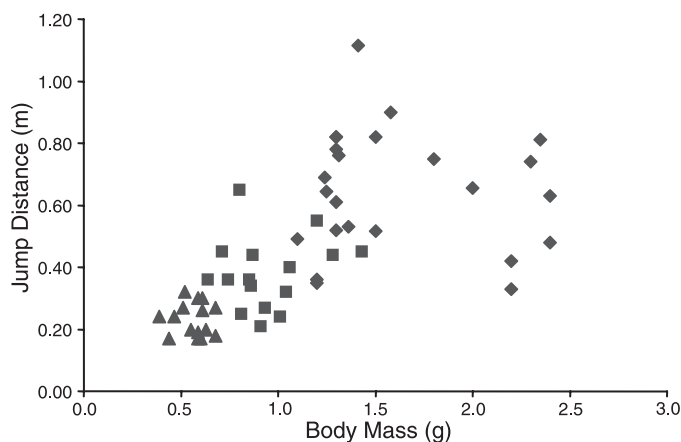


Fig. 3. A scatter plot from the class data of jump distance against body mass for adult and juvenile locusts. Diamonds, adult locusts; squares, 5th instars; triangles, 4th instars.

DISCUSSION

The locust provides a robust model for investigating the biomechanical, physiological, and anatomical principles underlying jumping. This practical exercise can be run at a number of levels of complexity, for example, at the simplest level by simple comparison of the distances traveled and the power produced during the jump compared with those produced by humans during a standing jump. The contractile properties of the muscle can be investigated and a comparison made between the power produced by the extensor muscle when stimulated to contract, in the absence of energy storage mechanisms, and that generated in vivo.

The main finding from these experiments is that the power generated by the intact locust during jumping is of the order of 1 W/g of muscle, which is ~ 50 times the maximum power generated by muscle contraction during electrical stimulation. Furthermore, the intact adult animal not only generates significantly more power than can a human athlete performing a standing jump, but this power output is also greater than the calculated maximum for active endothermic muscle, which is ~ 0.85 W/g (2).

Students can be asked to approach this problem from several perspectives. Standing jumps place special demands on the muscles because, to generate the required power for the jump, the muscle needs to contract rapidly and to generate large amounts of force. However, when muscle contracts rapidly, it only generates relatively low levels of force (14) and vice versa. Before the class, students can be asked to research the

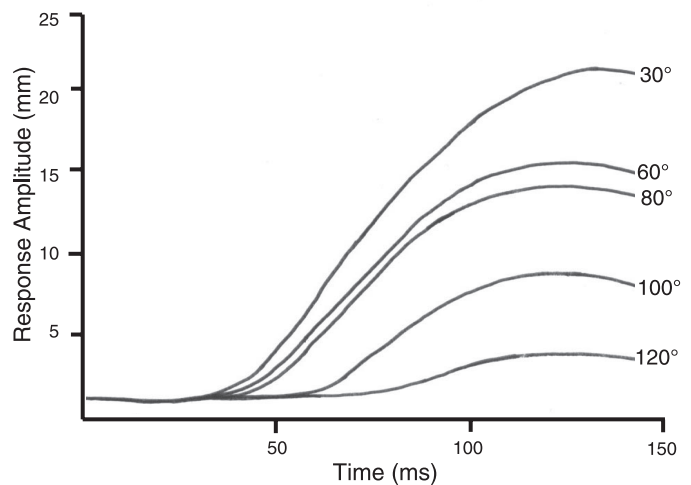


Fig. 4. Overlaid records of the rising phase of the movement of an isolated leg in response to direct stimulation of the extensor tibiae muscle starting from different femorotibial joint angles. Stimulus train: 5 pulses, 0.5 ms duration, at 20 ms intervals.

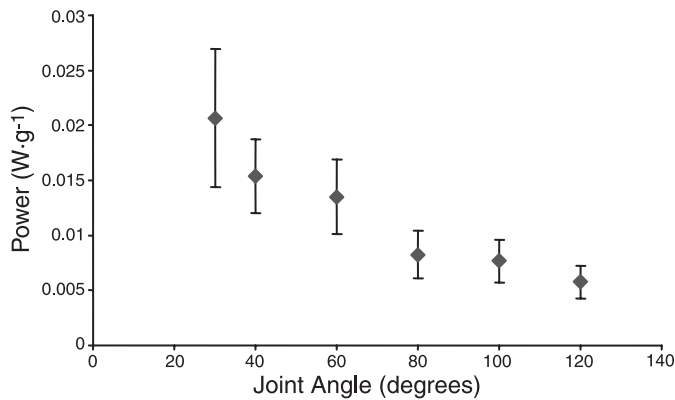


Fig. 5. Power output from the adult extensor tibiae muscle as a function of joint angle evoked by direct muscle stimulation. Error bars: SD; $n = 14$.

properties of muscle and the biomechanics of jumping in humans and use the research literature to draw up a set of ideal properties for the muscles and limbs powering the jump, for example, in terms of contractile properties (rate and force of contraction, etc.), pennation angle, limb length, etc. They can then compare these with the actual properties of the locust jumping leg. The discussion is then extended by using the research literature to investigate the range of adaptations displayed by the locust for the storage and explosive release of potential energy (1, 6, 12), in particular, the relatively large mass and the pennation angle of the extensor muscle, the length and elasticity of the extensor apodeme, and the mechanical properties of the semilunar processes.

A useful analogy for the locust jump is that of the archer shooting an arrow, i.e., during the preparation phase, the archer draws the bow back relatively slowly. Under these conditions the archer is able to exert a large amount of force because the shortening speed is relatively low. As a consequence, the power output is also relatively low. The drawing back of the bow stores potential energy as the elastic strain of the bow. When the arrow is released, it is with great power, because the bow recoils very rapidly, thereby exerting the force on the arrow over a very short period of time. Although the force during release is almost the same as the force exerted on the bow to draw it back, the power imparted to the arrow is very high because of the rapidity of the release.

Further discussion can focus on the behavioral implications of this mechanism, for example, any potential risk associated with the preparatory delay of up to 600 ms (1) and the inability of freshly molted individuals to jump (or kick) because the cuticle is too soft (16). Comparison of jumping between adults and instars enables insights into the effects of allometric growth on the mechanical systems, for example, by comparison of the changes in muscle volume (as approximated by measuring the dimensions of the femur) and lever ratios (8, 9). It is notable, from Fig. 3, that there is a linear relationship between body mass and jump distance when the instar and adult groups are taken together, indicating a scaling of performance. However, such relationships did not pertain within the age groups. One of the main factors contributing to this variability would be the stage of the individuals after the last molt. Immediately after a molt, the cuticle is soft and hardens over several days, thereby giving rise to a varying jump (16).

This variability could be reduced by only using locusts at specific stages of development.

Discussion of the results of the muscle stimulation can relate to the physiological properties of muscle as revealed in these experiments. For example, variation of the interpulse interval can show the effects of summation and also of the absolute and relative refractory periods. Likewise, changing the load on the isotonic transducer allows investigation of the relationships between power, shortening velocity, and work done.

The effect of the initial joint angle on the power output is marked by a steady decline in power output with increasing joint angle (Figs. 4 and 5). This is the result of two main factors. The first is the effect of sarcomere length on the force-length relationship (10). As the initial joint angle increases (i.e., the starting position is in extension rather than flexion) so the initial sarcomere length decreases and the prestretch on the muscle decreases. As a consequence, the contractile tension is reduced because the overlap of the actin and myosin filaments is no longer optimal. The second factor is the lever arm of the extensor muscle, which changes as the joint rotates. When the joint is flexed, the extensor lever arm is very low (6, 11). As the tibia extends, the lever arm rises to a peak at a joint angle of around 100° before declining rapidly again toward full extension. The relationship between these two factors is, therefore, complex. For starting angles up to $\sim 100^\circ$ the decreasing sarcomere length is reducing and the increasing lever arm is increasing the turning moment applied to the tibia. Beyond 100° both factors are leading to a reduction in the turning moment. However, the result appears to be a decline in power output over the joint angles tested (Fig. 5).

The undergraduate laboratory described in this paper enables a variety of biomechanical and physiological experiments to be undertaken by using the model of the locust jump. Students can carry out investigations at a number of levels to observe the effects of energy storage on the power generated by locusts to produce the jump, and they can study the contractile properties of muscle in a robust preparation.

APPENDIX: SAMPLE CALCULATIONS FOR THE POWER OUTPUT FROM JUMPING

Experimental measurements:

- Jump length (d) = 0.7 m
- Locust mass (m) = 1.6 g = 0.0016 kg
- Femur length (L) = 20.3 mm = 0.0203 m
- Mass of a single muscle = 0.076 g = 7.6×10^{-5} kg
- Acceleration due to gravity = $9.81 \text{ m}\cdot\text{s}^{-2}$
- Angle through which the leg joint moves = 130°

Step 1. Calculate the velocity (v) at takeoff.

d = distance traveled by locust

$$d = \frac{v^2}{g}$$

$$v^2 = dg$$

$$v = \sqrt{dg} = \sqrt{0.7 \times 9.81} = \sqrt{6.87} = 2.62 \text{ m}\cdot\text{s}^{-1} \quad (A1)$$

Step 2. Calculate the acceleration distance (s).

Length of the femur (L) = 0.0203 m

$$s = 2.27 L$$

$$s = 2.27 \times 0.0203 = 0.046 \text{ m} \quad (A2)$$

Step 3. Calculate the acceleration (a).

$$v^2 = 2as$$

$$a = \frac{v^2}{2s} = \frac{6.87}{0.092} = 74.67 \text{ m}\cdot\text{s}^{-2} \quad (\text{A3})$$

Step 4. Calculate the power (P).

$$P = \frac{v \cdot m \cdot a}{2} = 2.62 \times 74.67 \times 0.0016/2 = 0.16 \text{ W} \quad (\text{A4})$$

Step 5. Think about the units involved here.

acceleration, $a = \text{m}\cdot\text{s}^{-2}$

mass, $m = \text{kg}$

velocity, $v = \text{m}\cdot\text{s}^{-1}$

$$\therefore P = \frac{v \cdot m \cdot a}{2} = \text{m}\cdot\text{s}^{-2} \cdot \text{kg} \cdot \text{m}^{-1} \cdot \text{s}^{-1} = \text{kg} \cdot \text{m}^{-2} \cdot \text{s}^{-3} = \text{watts} \quad (\text{A5})$$

Step 6. Calculate the power output per gram of leg muscle.

$$P/2 = 0.16/2 = 0.08 \text{ W per leg} \quad (\text{A6})$$

Muscle weight = 0.076 g

Power output = 1.05 W/g⁻¹

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