THE ENERGETICS OF THE JUMP OF THE LOCUST *SCHISTOCERCA GREGARIA*

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SUMMARY

The anatomy of the metathoracic leg is redescribed with particular reference to storage of energy in cuticular elements and the way in which the stored energy is used in jumping.

The jump of adult male locusts requires an energy of 9 mJ and that of the female requires 11 mJ. The semilunar processes of each metafemur store 4 mJ at a stress of 15 N, and the extensor tibiae apodeme stores a further 3 mJ at the same stress. The total stored energy in both metathoracic legs is 14 mJ.

The extensor tibiae muscle produces a maximum isometric force of over 15 N at 30 °C and, when loaded with the extensor apodeme and semilunar processes, attains this force in 0·3 sec with a strain of 0·8 mm. The peak power output is 36 mW or 0·45 W.g^{-1}. The peak isometric force is attained when the tibia is fully flexed and the force falls as the tibia extends. The extensor tibiae muscle A band is 5·5 μm long and the peak force is over 0·75 N.m^{-2}. The peak velocity of shortening is 7 mm.sec^{-1} or about 1·75 lengths/sec at 30 °C.

The tensile strength of the extensor apodeme is 0·6 kN.mm^{-2} and Young's modulus is 19 kN.mm^{-2}. The safety factor does not exceed 1·2 and the safety factor of the semilunar processes and tibial cuticle is little higher.

The jump impulse lasts 25–30 msec. A velocity of 3·2 m.sec^{-1} is reached after a peak acceleration of 180 m.sec^{-2}. The peak power output is 0·75 W at close to maximum velocity. Energy losses in rotating the femur and tibia are small and it is shown that the leg is able to extend at 7 times the normal rate with losses of about 20%. Most of the stored energy is converted to kinetic energy as the animal jumps.

A model based on the relaxation of a spring that has the properties of the elastic elements of the locust leg into a lever with the same kinematics as the locust leg produces a force–distance curve similar to that measured for locust jumps. The major part of the jump energy is stored before the jump.

INTRODUCTION

Locusts of all instars jump. The neuromuscular physiology has been examined from various standpoints (e.g. Hoyle, 1955; Usherwood & Runion, 1970) and the energetics of the impulse and the forces produced during the jump have been examined (Hoyle, 1955; Brown, 1963). Neither of these two approaches has presented an

energy budget and described the mechanical events before and during the mechanical impulse produced by the extension of the two metathoracic legs nor attempted to relate these to the animal's biology.

The present work considers some of these problems; in particular I have examined the energy produced and power output, the forces produced before and during the jump, and the architecture and mechanical loading of the exoskeleton.

In a large animal, such as the dog, the muscle loading is arranged so that the muscle force is maximal at the start of the impulse and falls as the animal accelerates, thus producing a high energy output from a single contraction. The power that is produced is compatible with direct action of the muscles (Alexander, 1974). In a very small animal, such as the flea, the energy is compatible with that of a single muscle contraction but the power produced during the impulse is vastly greater. Prior to jumping, the animal remains motionless for over 0·1 sec, storing energy in a pad of resilin, and then jumps in 0·7 msec, releasing this energy (Bennet-Clark & Lucey, 1967).

In the locust, the jump results from the contraction of the large extensor tibiae muscles of the two metathoracic legs. These receive fast and slow motor neurones (Hoyle, 1955) and are activated prior to the jump (Brown, 1967; Godden, 1969). The twitch tension of the muscle reaches a maximum 20–30 msec after a single fast motor impulse (Hoyle, 1955), but the twitch force is far less than the force produced during the jump impulse and develops more slowly. In fast tetanus, force rises slowly and reaches a peak after some 500 msec. With the tibia flexed and the flexor muscle activated, extension is prevented by a catch formed by the flexor apodeme and a cuticular knob inside the femur (Heitler, 1974). Brown (1967) has suggested that the jump is initiated by relaxation of the flexor muscles, allowing energy stored in elastic elements of the extensor system to be released. This cycle of storage and release is considered here.

MATERIALS AND METHODS

The locust *Schistocerca gregaria* was cultured in 0·5 m cubical cages each fitted with 15 W lamps, in a room kept at between 27 and 29 °C. All lighting was controlled on a 12 h light/12 h dark cycle. Each cage contained a group of animals which had been laid as eggs over a 1-week period. After adult ecdysis, animals were placed in a different type of cage provided with jars of sand; about 70 adults of a given age group were kept in each cage. All instars were fed freshly cut grass and bran, with casual additions of herbaceous plants. Faeces and corpses were removed on week-days.

Adult female locusts from 14 to 28 days after ecdysis were used for the majority of experiments. The metathoracic legs of such insects have femora from 23 to 27 mm long but those with femora between 24 and 25 mm long were selected for quantitative experiments. Experiments on jump performance and muscle physiology were made in a constant temperature room kept at $30 \pm \frac{1}{2}$ °C.

The jumping performance was measured by placing animals on a platform at the centre of a large sheet of paper marked with concentric lines at 0·1 m radii out to 1·1 m radius. The surface of the platform was wound with a grid formed from a pair of insulated wires, glued to the surface and with the insulation removed over

the plane of the platform. This platform was electrified from a stimulator giving 60 V, 50 Hz pulses controlled by a switch. Locusts were placed or dropped on the centre of the platform and induced to jump from the platform by bursts of stimuli through their tarsi and in a particular direction by a light placed in front of the experimenter. Each locust was made to jump at least ten times and a period of at least 5 min was allowed between each stimulated jump. The range of each jump was estimated to the nearest 50 mm, and at the end of a series the animals were weighed.

Flight during the jump was prevented by taping the wings together with Sellotape. Jumping during weighing was prevented by removing the Sellotape and fitting a pair of plastic rings over the femoro-tibial articulation of the hind legs; Sellotape and rings weighed about 30 mg so the effective gross weight of the insect was unchanged.

The properties of the extensor tibiae and flexor tibiae muscles were measured using an Electrophysiological Instruments Wire Strain Gauge and amplifier. Two gauges, with 5 and 50 g ranges, were employed. Both were substantially linear. The 50 g gauge had a rise time of under 5 msec and a slewing rate of over 10 g.msec^{-1}. Under full load, the deflexion was about 1 mm. Before use, both gauges were calibrated with an appropriate weight. In use, they were connected to the tibia of the preparation by a length of polyester thread of negligible weight and negligible strain under the stresses involved.

In an experiment, the leg was removed from the locust at the coxa, and, depending on the experiment, the flexor apodeme was either cut at its tibial end or left intact. The leg was pinned to a shaped piece of balsa wood so that it was clamped externally at the distal end and transfixed at its proximal extremity by a pair of stainless-steel pins which also acted as stimulating electrodes. Stimulation at frequencies up to 100 Hz was provided by an Electrophysiological Instruments stimulator which was controlled by a morse key. The level was set to just above that which produced a reliable contraction of the extensor tibiae muscle.

Oscillograms were recorded using a Telequipment D53A oscilloscope and Nihon Kohden camera type PC2B. Records were made directly off the outputs of the strain gauge and stimulating electrodes.

Strains in the femoral cuticle were measured using a calibrated micrometer microscope. Stresses were applied either by loads connected to the proximal end of the tibia by slings made of polyester thread or by stimulation of the extensor tibiae muscle and measurement of the force produced at a known distance along the tibia. The mechanical advantage of the flexor and extensor muscles at the distal end of the tibia was measured by pinning the femur, with one side dissected off, to a piece of balsa wood, with the tibia describing an arc about the centre of a paper protractor pinned to the wood. The broken ends of the two apodemes were pulled with forceps and the distance moved against angular movement of the tibia was recorded.

Tensile strength of the extensor tibiae apodeme was measured either by calculation from the force produced at the distal end of the tibia by a muscle contraction, or by loading the tibia via a sling of polyester thread. In the latter case, the suspensory ligaments of the femoro-tibial articulation were cut, the spines along the tibia were

removed, and a sling was passed around the ventral side of the proximal end of the tibia. The femur was then clamped with the tibia flexed between two shaped pieces of balsa wood and the load was applied symmetrically between the two pieces of wood and the tibial sling, using the screw of a Palmer stand and a spring strain gauge as the upper moving suspension point.

Attempts were made to mount short lengths of apodeme between strips of glass using Araldite adhesive and symmetrically placed polyester thread attachments. These gave low values for the Ultimate Tensile Strength (U.T.S.).

Young's Modulus for the extensor tibiae apodeme was measured by bending it with a piece of watch hairspring. A 5 mm length of spring was mounted on a platform at one end of a microscope slide and was calibrated by measuring its deflexion under load from a fixed pin. The test piece of apodeme was fixed with dental wax to a similar platform held with grease on the centre of the slide. By sliding the apodeme against the spring, known loads were applied and the deflexions of apodeme and spring were measured. The length of the loaded portion was measured and the apodeme was broken near the fixing point so that the thickness and width of the beam could be measured.

Jumps were filmed with the assistance of, and using a set-up devised by, E. C. A. Lucey. A Fastax camera set to run up to 1500 frames/sec was fitted with a Wollensak lens of aperture $f2$ and focal length 52 mm. The insect was placed on the electrified platform described earlier and a back-illuminated grid of squares at 20 mm intervals was placed 30 mm behind the insect. The camera was focused on the insect and the camera-to-insect distance was noted. Further illumination was provided by an overhead spotlamp and one aimed obliquely at the front of the insect.

In a filming run the lights were turned up, an insect was taken and held about 0·1 m above the electrified platform, which was continuously energized, the camera was started and, after $\frac{1}{2}$–1 sec, the insect was dropped on to the platform, facing across the field of view of the camera. Jumping usually occurred within the 3 sec of filming time that remained on the 100 ft film run.

Filming was carried out at apertures of $f4$ and $f5·6$ on Ilford HP 4 stock. Time markers were photographed during the run at 1 msec intervals. The effective exposure of the Fastax rotating prism shutter is one-third of the frame interval.

Six jumps were filmed. These were measured using a Lytax frame analyser and tracings were made, frame by frame. Correction was made for the 30 mm difference between the distance of the insect and the distance of the 20 mm grid from the camera.

Owing to imprecise framing it was hard to measure the distance moved at the start of the jump, and because of the relatively long exposure of each frame it was hard to define the position of the insect at the end of the jump. This leads to such anomalies as the apparent acceleration of an airborne insect (Fig. 14).

The weight of the insects was recorded and, between film runs, they were kept at about 30 °C using an infra-red lamp. As it was impracticable to heat the film studio above 20 °C and as the lighting provided considerable heat, the temperature of the insect at the time of jumping is not known but was probably between 25 and 33 °C.

S.I. units are used. As the error involved is only 2 % I have assumed that a force

of 10 N is equivalent to a weight of 1 kg and that an acceleration of 10 m.sec^{-2} equals 1 standard gravity (1 g).

Where the term impulse is used, it applies to the mechanical event which causes the animal to accelerate from rest by an extension of the metathoracic legs. The term is not used as a measure of the change of momentum which accompanies a blow.

RESULTS

1. *Anatomy of the locust and its metathoracic leg*

The general anatomy of the locust has been well described elsewhere (e.g. Albrecht, 1953). The position of the centre of gravity was found by passing a pin through newly killed adult locusts. In both sexes and regardless of age, the centre of gravity is within 2 mm of the centre of a line joining the ventral ends of the metapleural ridges. Thus, so long as the metathoracic coxae are depressed throughout the jump, the majority of the energy of the impulse can be produced by a simple extension of the metathoracic tibiae and this impulse will produce only a small torque on the body of the insect.

The metathoracic legs are specialized for jumping. The femur is expanded dorsoventrally and contains dorsally the large extensor tibiae muscle (135) and ventrally the smaller flexor tibiae muscle (136), as well as accessory muscles and the retractor unguis muscle (Fig. 1 B) (Snodgrass, 1929).

The cuticle of the femur is reminiscent of the Tour d'Eiffel and is similarly adapted to withstand longitudinal loads by the presence of skeletal ridges along the angles of the column. Between these ridges the thinner flat surfaces are scalloped into a series of facets which form dorsally the outer attachments of the extensor tibiae muscle blocks and ventrally the smaller attachments of the flexor tibiae muscle (Snodgrass, 1929).

The distal end of the femur bears the specialized articulation with the tibia. The tibia is suspended by a pair of short straps of flexible cuticle from the end of the paired dark semilunar processes, below which are a pair of pale-coloured plates which cover the head of the tibia when this is flexed (Fig. 1 A). The semilunar processes are highly sclerotized and are joined to the more proximal part of the femur by a ring of thick but less brittle cuticle which forms a neck before the expansion that contains the large extensor and flexor muscles. Dorsally, the two semilunar processes are joined by an arch of thickened cuticle, and ventrally they are joined to the cover plates by a flexible cuticle (Fig. 1 A, Fig. 5).

The semilunar processes are composed of thickened cuticle; the crescent seen on the outside is continued as a banana-shaped thickening internally (Fig. 1 B). When this is fractured, the lamellae can be seen. These run longitudinally, parallel to the inner surface, and are about 1 μm thick. The average weight of a semilunar process is 1.3 ± 0.2 mg.

The ring of cuticle that carries the semilunar processes and cover plates bears a dark cuticular invagination on its ventral distal margin. Internally this structure is thickened by a layer of resilin (Weis-Fogh, 1960) to form a roughly hemispherical lump which acts as a catch for the flexor apodeme when the tibia is fully flexed
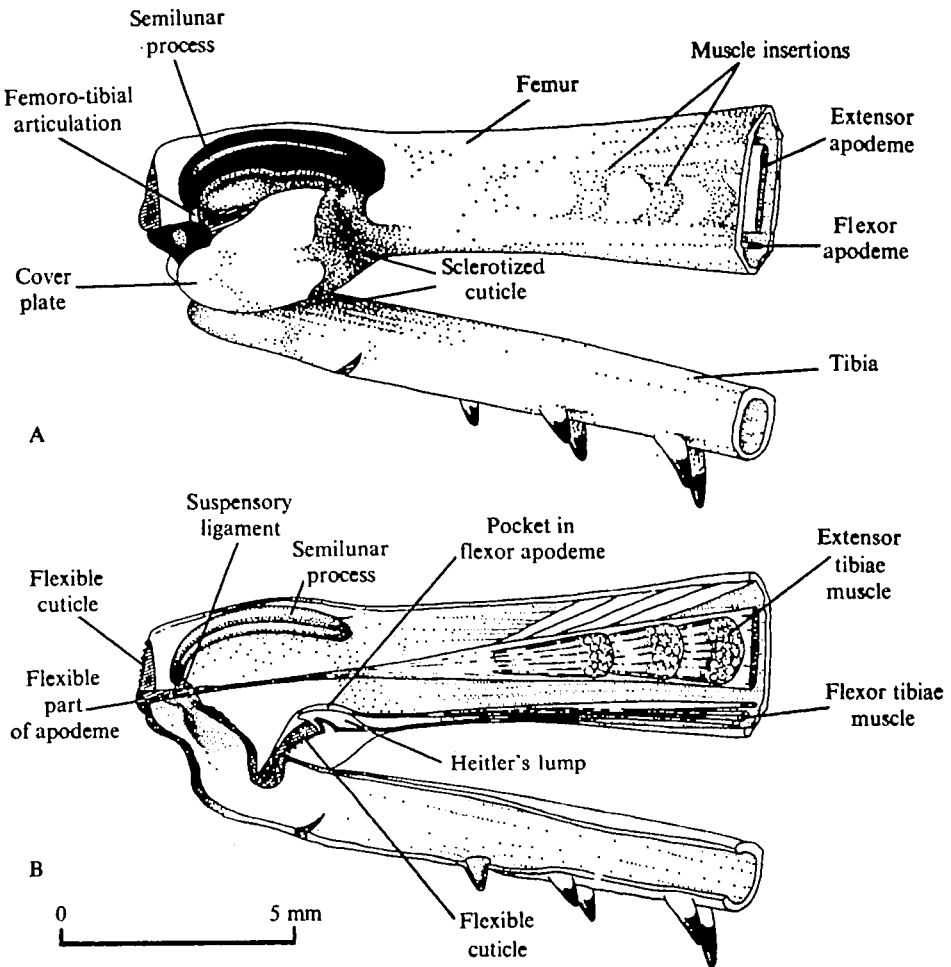
Fig. 1. Diagram of the metathoracic leg of the locust to show the anatomy of the femoro-tibial articulation and the specializations for jumping. (A) External anatomy, showing the tibia suspended from the distal ends of the semilunar processes and the heavily sclerotized cuticle either side of the articulation. Flexible cuticle is shown cross-hatched. (B) Simplified internal anatomy showing the larger extensor apodeme and the pinnate extensor tibiae muscle, the flexor apodeme and the specializations forming the catch that holds the leg flexed. The internal thickening of the semilunar process is shown. For simplicity, the tracheae and minor muscles of the tibia and tarsus have been omitted.

(Heitler, 1974) (Fig. 1 B). When manipulated, this lump is extremely slippery and feels rather like synovial cartilage.

The tibial articulation is by flexible cuticle attached to lateral expansions at the distal ends of the semilunar processes. Dorsally, the cuticle continues as a thin flexible region similar in appearance to the skin of a human knuckle, and ventrally, between the cover plates, as a very thin and delicate flexible cuticle with extensive stellate folding. Full extension of the tibia is through an angle of between 140 and 150°, and this is accompanied by a small amount of folding dorsally and the stretching of a far greater area ventrally.
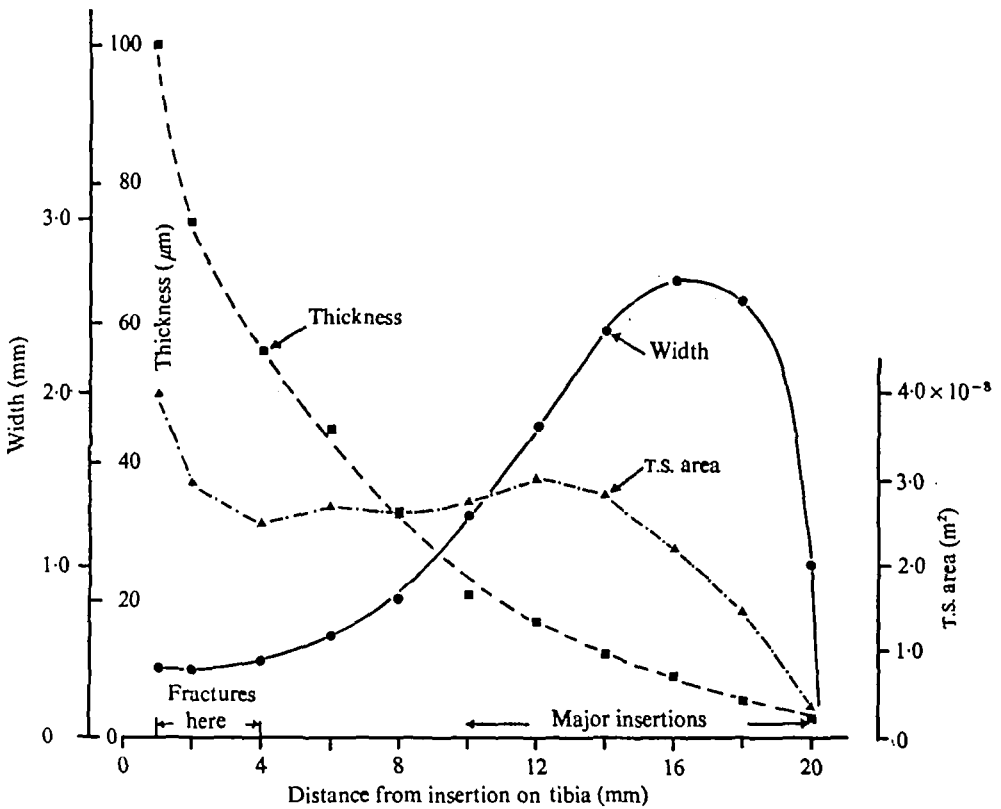
Fig. 2. Graph of width, thickness and T.S. area against distance from the insertion on the tibia for the extensor tibiae apodeme from a locust metafemur 24–25 mm long. The region where fractures occur following muscle stimulation and the region where 90 % of the muscle fibres insert are indicated on the abscissa.

The principal apodemes of the muscles moving the tibia are specialized. The extensor apodeme, which inserts over an arc of the apex of the tibia, forms a strap which runs horizontally through the ring that supports the semilunar processes, and then twists to run vertically between the muscle blocks (Fig. 1 B). As the area of the outer muscle insertions increases towards the proximal end of the femur, so too does the surface area of the extensor apodeme increase; as it becomes broader so it becomes thinner and, over most of its length, the area of cross-section remains constant (Fig. 2).

The extensor muscle is inserted over most of the surface of the apodeme; with the tibia flexed, the angle of insertion is about 20° so the probable effective area of cross-section of the muscle is sin 20° or 0·34 times the surface area of the apodeme.

Apodemes were prepared by boiling and by dissection of fresh legs. The average surface area for a femur 24–25 mm long was 48 ± 4·6 mm² so the effective area of cross-section of the muscle with the legs flexed and relaxed is 16·2 mm².

The extensor apodeme is composed of a brittle cuticle which is hard to manipulate. Fractures examined under the Scanning Electron Microscope show that the structure is fibrous with a preferred orientation along the apodeme and that the fibres appear

to be fused together. The material fractures readily either transversely or longitudinally but with little of the splintering that happens with wood (Bennet-Clark, 1975).

The flexor apodeme is formed from a pair of heavily sclerotized strips which arise from either side of the tibia and converge after about 1 mm to form a strap-like apodeme. At the convergence, the apodeme is thin and flexible. This region forms the pocket that engages on the resilin lump to form the catch (Heitler, 1974).

If the tibia is pulled away from the femur, the extensor apodeme usually snaps somewhat distal to the muscle insertions (Fig. 2), but the flexor apodeme comes out intact, surrounded by torn muscle. The extensor muscle is stronger than its apodeme but the flexor apodeme is stronger than its muscle.

The tibia shows a variety of specializations. Although, superficially, the shaft appears to form a simple cyclindrical tube, it is strengthened in various ways. Along the length of the ventral side, the compression side in the kick, the cuticle is more heavily sclerotized. The cuticle is less thick towards the distal end (Jensen & Weis-Fogh, 1962). The dorsal side is armed with a double row of heavy fixed spines which increase the rigidity of the tube (Alia & Crovetti, 1961). At the distal end of the tibia are two pairs of strong spurs, set on sockets of flexible cuticle, which only allow backward bending of the spurs.

The proximal end of the tibia is bent to form an articular region set at right angles to, and some 2 mm ventral to, the axis of the tubular region. There are two wide lateral expansions on which the suspensory cuticular straps insert, proximal to which is the broad flexible insertion of the extensor apodeme, and distal to which are the paired insertions of the flexor apodeme. At this end of the tibia, the cuticle is thick and heavily sclerotized but, because of the various apodemes, only becomes tubular distal to the insertion of the flexor apodeme (Fig. 1 B). Near the proximal end of the tubular region there is a dorsal band of lightly sclerotized cuticle which allows the tibia to bend slightly when fully flexed (Fig. 1).

The bulk of the tibia is filled by a large trachea. The few muscles are all small. The tibia thus acts as a hollow tubular strut. Its length in female locusts is 23–24 mm, and the weight of tibia and tarsus is from 22 to 24 mg.

The femur contains the large extensor tibiae, the smaller flexor tibiae and a number of smaller muscles of the tibia that are of lesser importance in jumping.

The extensor tibiae muscle, Snodgrass's 135a and b (1929), which is highly pinnate, inserts over all but the distal 5 mm of the 20 mm long extensor apodeme. Its fibres vary in length along the femur from 2·5 to 4·3 mm with the leg relaxed and flexed, but the shorter fibres are only found in the distal part of the femur, and over 80 % of the muscle volume has fibres between 3·7 and 4·3 mm long. The muscle weighs 70 ± 6 mg in female locusts, so, assuming a density of 1 mg.mm^{-3}, the effective area of cross-section is about $\frac{70}{4}$ mm^2 or 17·5 mm^2, which agrees closely with that calculated earlier on the basis of the angle of the insertion and the area of the apodeme.

The flexor muscle, Snodgrass's 136 (1929), weighs about 15 mg and consists of fibres between 6·5 and 7 mm long with the leg relaxed and flexed, so its effective area of cross-section is about 2·2 mm^2.
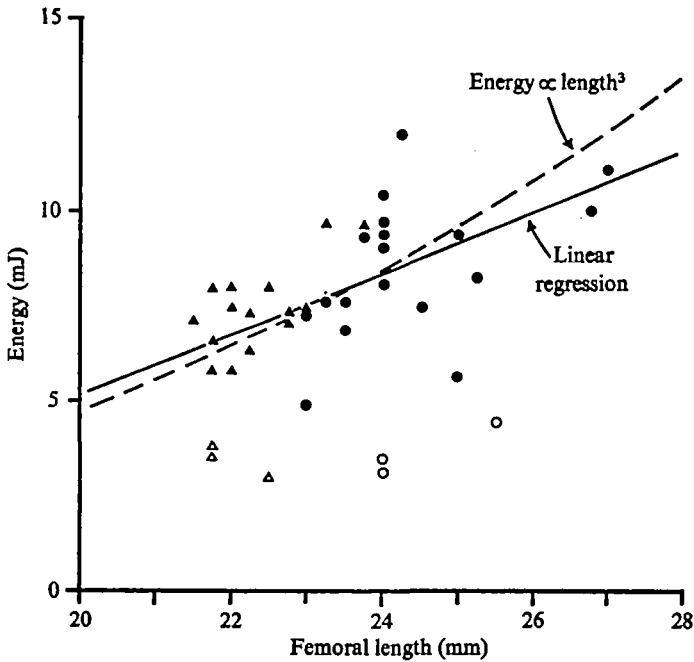
Fig. 3. Graph showing jump energy against femoral length for adult locusts. Each point is calculated from the distance jumped in the best of ten jumps by one insect at 30 °C. The continuous line shows a linear regression of jump energy on femoral length and the dashes show a line calculated on the assumption that energy is proportional to femoral weight: there is no significant difference between these two lines. △, One-legged males; ○, one-legged females; ▲, two-legged males; ●, two-legged females.

2. *The normal jumping performance*

A group of 15 male and 15 female locusts were taken between 10 and 14 days after the last moult. The same animals were tested 1 week later.

The assumption is made that for the longest range, the angle of take-off is 45°. The energy of the impulse is given by

$$E = \frac{m.g.d}{2\sin 2\theta},$$
(1)

where E is the energy in Watts, m is the mass in kg, g is the acceleration due to gravity (9.81 m.sec^{-2}), d is the horizontal range in metres, and θ is the angle of take-off in degrees above the horizontal. This approximates to

$$E = 5m.d.$$
(2)

The results for the individual locusts are plotted against the length of the meta-thoracic femur (Fig. 3); it will be seen that a linear regression line drawn through the points corresponds closely to the position of a line drawn on the assumption that femoral weight is proportional to femoral muscle energy and to the cube of femoral length.

A male locust jumps a horizontal distance of 0.8–0.95 m and weighs 1.5–2 g.

A female jumps 0·5–0·7 m and weighs 2·5–3·5 g. The effective initial velocity can be calculated from

$$V = \frac{d.g}{\sin 2\theta},\tag{3}$$

giving an initial velocity of between 3·1 and 2·2 msec^{-1}. The time taken to describe the range is given by

$$t = \frac{2V \sin \theta}{g},\tag{4}$$

where t is in seconds, which, for the range of velocities calculated above, gives a time of 0·43–0·31 sec.

The effect of air resistance can now be estimated. Assuming the worst case of a trajectory normal to the insect's long axis and the maximum initial velocity, the drag force (P) can be calculated from

$$P = 1·3r.l.V^2,\tag{5}$$

where r is the radius and l is the length of the body and V is the velocity (Alexander, 1971). A female locust is about 10 mm in diameter and 60 mm long, a male about 8 mm by 50 mm. The maximum force in the worst case is 3·7 mN but a rather lower force of around 2·5 mN seems more likely, as the animal tends to align itself in the direction of movement (Pond, 1972).

The final velocity can be calculated from the initial velocity and the deceleration in m.sec^{-2} is given by

$$f = P/m,\tag{6}$$

which for a male locust gives 1·33–1·67 msec^{-2} and for a female locust 0·7–1·0 m.sec^{-2}. This acts over the time of the trajectory to reduce the velocity. If it is assumed that the velocity calculated from the range (formula 3) is the average velocity, this is the velocity at mid-range. The initial velocity will be

$$V_{1n} = V_{av} + \frac{f.t}{2},\tag{7}$$

and the final velocity will be

$$V_f = V_{av} - \frac{f.t}{2},\tag{8}$$

where t is calculated from formula (4), V_{av} is calculated from formula (3) and V_{1n} and V_f are the initial and final velocities respectively. For a 3 g female locust the initial velocity is 2·63 m.sec^{-1} falling at landing to 2·37 m.sec^{-1}, and for a 1·7 g male the figures are 3·42–2·78 m.sec^{-1}.

The energy of the jump was measured on the basis of the range which has been used to calculate the average velocity. The energy lost in air resistance can be calculated from

$$E = \frac{m(V^2{}_{1n} - V^2{}_{av})}{2},\tag{9}$$

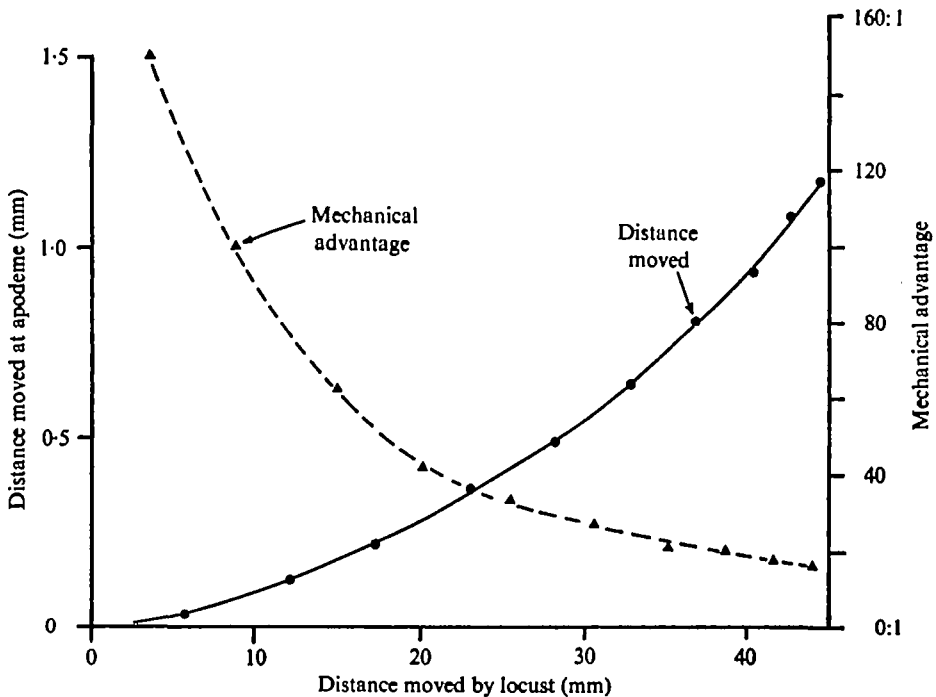which for a male locust gives 1·8 mJ and for a female locust 1 mJ loss.

Fig. 4. Graph showing the relation between movement at the extensor tibiae apodeme and movement of the distal end of the tibia from the proximal end of the femur for 24–25 mm locust metafemora. The mechanical advantage of the movement is obtained by differentiating the graph for distance.

The data in Fig. 3 show the energy required for the jump assuming that there is no air resistance. On the basis of the air resistance if the animal travels with its long axis normal to the trajectory, this represents an underestimate of some 20 %. It thus appears that a male locust produces between 7 mJ (Fig. 3) and 9 mJ allowing for air resistance, and that a female locust produces between 9·5 and 11 mJ. These values will be used later to establish the energy budget.

A one-legged insect jumps about half as far as the normal two-legged insect, and so the two legs appear to contribute equal amounts of energy (Fig. 3).

If an operation is made to remove Heitler's lump from the flexor catch mechanism, the insect will still jump but the range is greatly reduced and the accuracy of small hops appears to be less good. As the animal jumps, it no longer makes the sharp sound that accompanies the normal jump.

If the tibia is prevented from flexing fully, by a lump of Plasticine on the femur, the ability to jump is lost when the initial extension exceeds about 7° and, indeed, the animal will not try to jump.

When animals are stimulated to jump repeatedly from an electrified platform they become fatigued, and after the 5th to 10th jump the range falls until, after 20–30 jumps, the animal no longer jumps. In this condition they have been observed to autotomize a metathoracic leg and to get tangled up with their tarsal claws. Despite the strong stimulus, some of the older female insects were not readily induced to
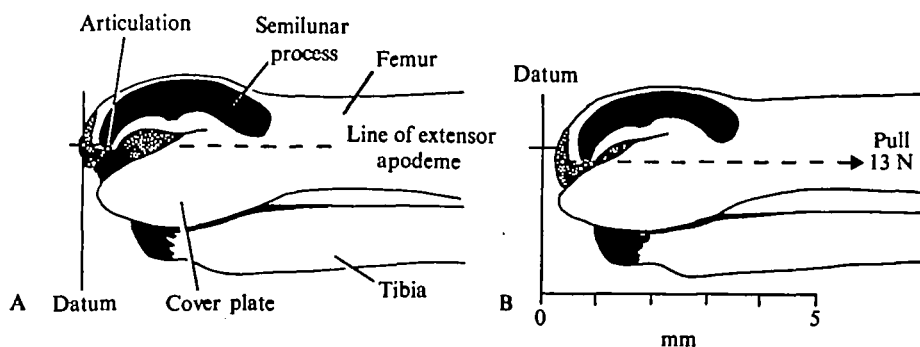
Fig. 5. Diagram showing the strain of the semilunar processes of the locust metafemur, traced from photographs. (A) The extensor tibiae muscle is not stimulated and the semilunar processes do not strain. The datum circle shows the attachment of the extensor apodeme to the tibia. (B) The extensor tibiae muscle is stimulated and the tibia is prevented from extending. The semilunar processes strain ventrad and proximad through about 0·4 mm, pulling the distal ends of the semilunar processes down between the cover plates and pulling the tibia ventrad away from the femur. The same datum is used as in (A). The stippled areas are flexible cuticle and the black areas are heavily sclerotized cuticle.

jump but walked off the platform or found a position where they could lift their feet off the electrified parts of the platform.

In over 500 jumps made from the platform only one insect spontaneously snapped its extensor tibiae apodeme. In the course of handling many hundreds of locusts, this has only been observed on two other occasions.

3. *Mechanical advantage of the femoro-tibial articulation*

This has already been measured by Heitler (1974). I have re-examined this from the particular aspect of the relation between movement of the extensor apodeme and movement of the whole insect. This is shown in Fig. 4, which also shows the angle of extension and the effective mechanical advantage (distance at apodeme/ distance moved by insect) of the tibia. At 7·5° the mechanical advantage is about 150:1 (Heitler gives 260:1 at 0°) and falls to 24:1 at 90° and 17:1 at 135°. These figures correspond closely with those of Heitler after allowing for the differences in the method of measurement; Heitler measured at right angles to the distal end of the tibia, whereas I have measured the chord of the arc described by the tibia. Heitler gives a mechanical advantage of 35:1 at 90° extension where my measure of 24:1 multiplied by tan 45°, the angle between the chord and the arc at 90° extension, gives 34:1.

At 90° extension the extensor apodeme runs normal to the shaft of the tibia. If a cord running parallel to the apodeme is attached to the distal end of the tibia the effective mechanical advantage between that cord and the extensor apodeme is 35:1 at all angles of extension of the tibia.

The mechanical advantage of the flexor apodeme is least when the leg is fully flexed. At an extension of 7·5° it is 12·5:1, and at 90° 25·5:1. Thus the flexor can hold the force of the extensor at small angles of extension but cannot hold at extensions above about 12–20° (Brown, 1967; Heitler, 1974).
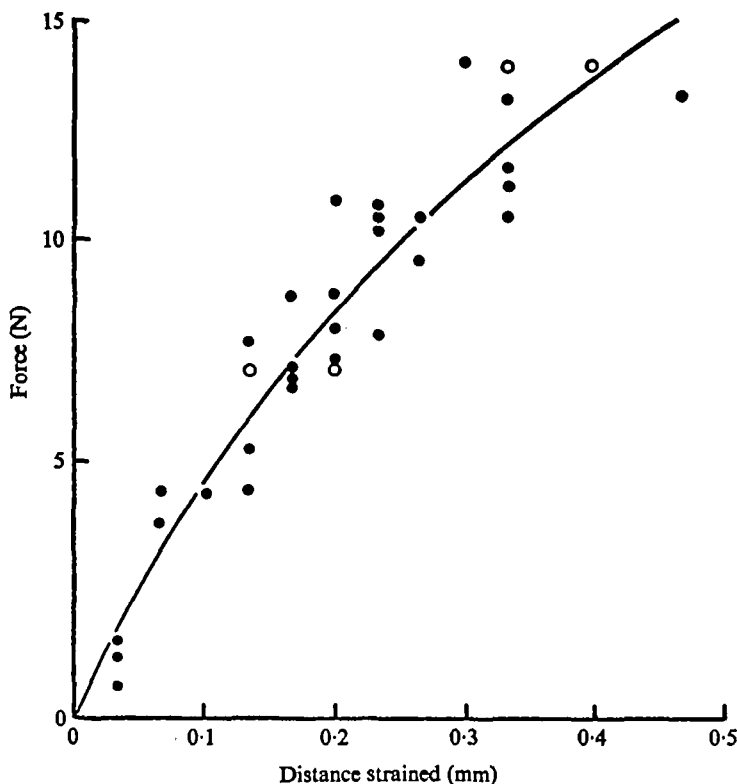
Fig. 6. Graph of stress against strain for the paired semilunar processes of locust meta-femora. Strain is measured along the axis of the extensor apodeme and the legs were stressed in two ways. ○, Points obtained by loading the proximal end of the tibia using a cord sling. ●, Points obtained by stimulating the extensor tibiae muscle and measuring the force produced at the distal end of the tibia.

4. *Mechanical properties of the semilunar processes*

When a locust struggles, attempts made to extend a metathoracic leg cause the two semilunar processes to be pulled inwards and downwards; this looks like a clenched fist being clenched more tightly (Fig. 5). The stress–strain relationship of this event has been examined by stimulating the extensor tibiae muscle with the leg constrained and by external loading, with measurement of the strain parallel to the extensor apodeme (Fig. 6). Maximum strains of over 0·4 mm have been observed but, at these high stresses, it is hard to hold the femur firmly without damage, and a muscle stimulated and producing such a stress fatigues in a few seconds.

The stress–strain curve is not linear. The energy that is stored is the product of force × distance over the curve of Fig. 6. This is given by the area below the stress–strain curve, which gives a stored energy of 4·05 mJ. If the semilunar processes behaved as Hookean springs, the energy, E, would be given by

$$E = \frac{\text{peak stress} \times \text{peak strain}}{2}, \tag{10}$$

which gives 3·5 mJ. These figures are substantially less than the 5–5·5 mJ required for the jump.

If the surface cuticle of the semilunar processes is scatched or nicked with a scalpel, a tranverse fracture occurs when the animal next tries to jump. When a fully flexed leg is stimulated to self-fracture, the fracture normally occurs at the extensor apodeme but fracture at the semilunar processes has been observed. External loading to destruction usually breaks the head of the tibia, the suspensory ligaments of the tibia, or the femur proximal to the semilunar processes; such fractures always occur if the load exceeds 17 N but loads of 14 N are sustained for several seconds. No plastic deformation has been observed during the time course of my experiments and it seems likely that, as the animal frequently but briefly stresses the semilunar processes with 15 N, plastic deformation of this highly sclerotized and highly elastic cuticle does not occur in the natural situation.

The semilunar processes weigh 1·3 mg each and so store about 1·5 J.g^{-1}.

5. Mechanical properties of the extensor tibiae apodeme

It has been notoriously difficult to measure the tensile strength of the extensor apodeme 'since only the insect is able to make attachments to it which do not cause it to break' (Brown, 1963). A fresh locust leg will break the apodeme if the leg is stimulated fully flexed or extended through not more than 15°. In this situation the force produced by the extensor tibiae muscle exceeds 14 N (see section 8) but is probably not above 17 N. When loaded thus, the apodeme breaks about 2 mm from the point of insertion on the tibia.

When external loads are applied it is difficult to apply these symmetrically, smoothly and rapidly enough to avoid tearing or shock loading. On many occasions the preparation broke either at the head of the tibia or in the proximal part of the femur under stresses of 9–11·5 N, leaving the extensor apodeme intact. On two occasions the extensor tibiae muscle tore at a stress of 14 N and was pulled out with the apodeme, and in one case the apodeme broke near the tibial insertion at the same load. The ultimate tensile stress of the apodeme is probably not less than 14 N and not more than 17 N.

In the region distal to the muscle attachments the apodeme is 0·5 mm wide and 50 μm thick, giving an area of cross-section of 0·025 mm^2. Thus the U.T.S. of the apodeme is between 0·56 and 0·68 kN.mm^{-2}, which is higher than that of mild steel and of the same order as silk or terylene (Jensen & Weis-Fogh, 1962).

The Young's modulus of a homogeneous brittle material is most simply measured by bending a beam fixed at one end with a load applied at the other. Young's Modulus, E, is then given by

$$E = \frac{Pl^3}{4d.a^3.b} \, \text{N.m}^{-2},\tag{11}$$

where P is the stress, l is the length stressed, d is the deflexion, a is $\frac{1}{2}$ the thickness in the plane of bending and b is $\frac{1}{2}$ the width normal to the plane of bending of a beam of rectangular cross-section.

In experiments it was found that specimens longer than about 3 mm twisted under load. The specimens tended to taper appreciably even in this short length (Fig. 2) and so there is considerable variability in the measurements. Readings were made with a series of test pieces, attached either at their thinner or their

thicker end; those that tapered towards the load tended to bend evenly along their length whereas those loaded at the thick end bent more sharply near the fixed point. The value quoted below is the mean for two samples of six in each of the two conditions.

Typical test pieces were 3 mm long and about 0·25 mm wide and varied in thickness from 30 to 50 μm. These deflected around 0·5 mm with loads of 2 mN.

Test pieces loaded for upwards of 10 min showed a further slow deformation of around 10 % of the initial deflexion, which recovered completely within 2 min of unloading. There did not appear to be any lasting plastic deformation and indeed this would be disadvantageous.

The average Young's Modulus found by this method is 18·9 ± 8·9 kN.mm^{-2}, so the apodeme is capable of elongating elastically by some 3·2 % when loaded to the U.T.S. of 0·6 kN.mm^{-2}. It seems likely from the width of the apodeme available for muscle attachment (Fig. 2) that the full force of 15 N is applied to the distal 10 mm of the apodeme and that an average force of half that is applied to the remaining 10 mm of the apodeme. Thus the apodeme will strain some 0·32 mm in the distal 10 mm and a further 0·16 mm in the proximal 10 mm, and the energy that is stored, from formula (11), is 2·4 + 0·6 mJ – a total of 3 mJ per leg.

The apodeme stores a substantial part of the total energy required for the jump. The estimate given above is subject to the following uncertainties: firstly, the properties of a beam in tension and in compression are only similar with a homogeneous material, and the apodeme is fibrous; secondly, it is not certain, and would be difficult to determine, how the force is distributed along the apodeme; thirdly, it would be hard to determine what the stress–strain properties of the apodeme are with large stresses because of the extreme brittleness of the material; and fourthly, the time course of the release of energy is not known.

On the basis of a density of 1·2 mg.mm^{-3} the energy that is stored in tension in 1 g of apodeme is 7·5 J. The energy stored in the semilunar processes is 1·5 J.g^{-1} but these act in shear where far lower values for the energy storage are likely.

6. *Cuticular strains in the femur*

As the extensor and flexor tibiae muscles contract, they produce a force which is approximately balanced about the suspension of the tibia. The femur will be compressed axially but there will only be small bending moments. No axial strain of the femoral cuticle proximal to the semilunar processes has been observed; if it occurs, the strain is probably less than 0·05 mm.

There is a small lateral strain of the outer cuticle of the femur in the region where the more ventral blocks of the extensor tibiae insert on the herring-bone facets of the anterior and posterior sides of the femur. As the muscle contracts, the centre of these facets deflects inwards through about 0·2 mm at the peak stress of 15 N. Assuming that the muscle fibres contract to a length of 3 mm and pull each side of the femur in through 0·2 mm, the width of the femur changes from 2·65 to 2·25 mm. At this stage the angle of the muscle insertions on the apodeme is 22·1°; if the tibia extends, allowing the sides of the femur to return to the original position without change in muscle fibre length, the angle of the muscle insertion on the apodeme rises to 26·2°, accompanied by a longitudinal movement of the apodeme of 0·1 mm. If all
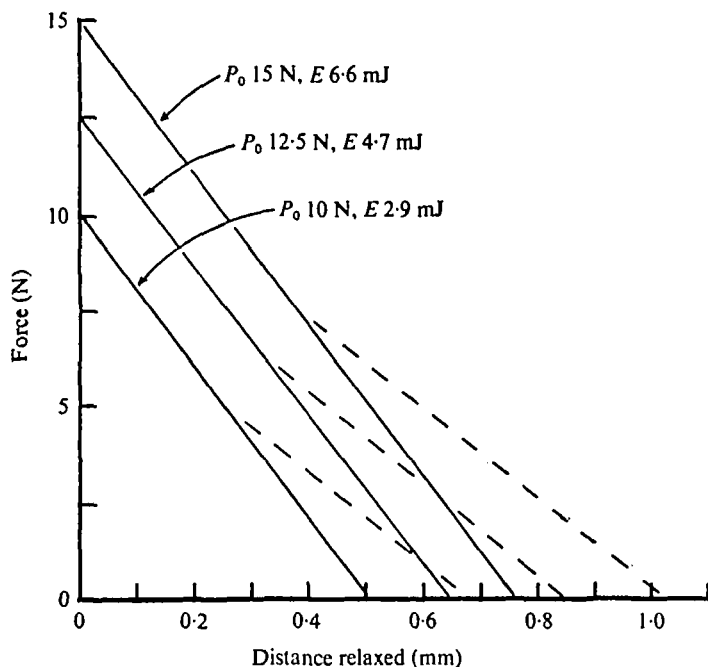
Fig. 7. Graph of stress against strain for linear springs with the properties of the elastic cuticular elements of locust metafemora. Continuous lines show the stress–strain relations for the semilunar processes and distal 10 mm of the extensor apodeme. The dashes show additional strain in the lateral walls of the femur and proximal end of the extensor apodeme. In drawing the graph it is assumed that the springs have been strained along the long axis of the femur by the stress P_0 shown on the ordinate and that as the stress is reduced the springs relax through the distance shown on the abscissa. The energy that is stored is given by the area under each line.

the extensor tibiae muscle was involved, the energy stored, from formula 11, would be 0·75 mJ, but this effect is only noted over about one-third of the outer muscle insertion and so the energy involved is unlikely to exceed 0·3 mJ.

7. Energy stored in the cuticle

At the peak stress of 15 N, 4·05 mJ is stored in the semilunar processes, 3 mJ in the extensor apodeme and a possible 0·3 mJ in the walls of the femur. The total is 7·35 mJ per leg, which is larger than the 5·5 mJ calculated on the basis of the jumping performance (section 2). The calculation of energy storage is based on stress up to the limit imposed by the tensile strength of the extensor apodeme and close to the limit of the semilunar processes. The energy released in jumping appears to have been preceded by stressing of the cuticular elements to $\sqrt{(5\cdot5/7\cdot35)}$ or 0·87 of the limit; the safety factor appears to be only 1·15:1, which is clearly acceptable if the forces decrease throughout the impulse as happens where stored energy is released.

It has been shown in section 4 that the 15 N stress of the extensor tibiae muscle causes an axial strain of 0·46 mm in the semilunar processes. It is postulated that this force produces a strain of 0·3 mm in the distal region of the extensor apodeme (section 5), while lesser forces and strains exist in the proximal part of the apodeme and the walls of the femur, accounting for a further 0·26 mm of axial strain at lower
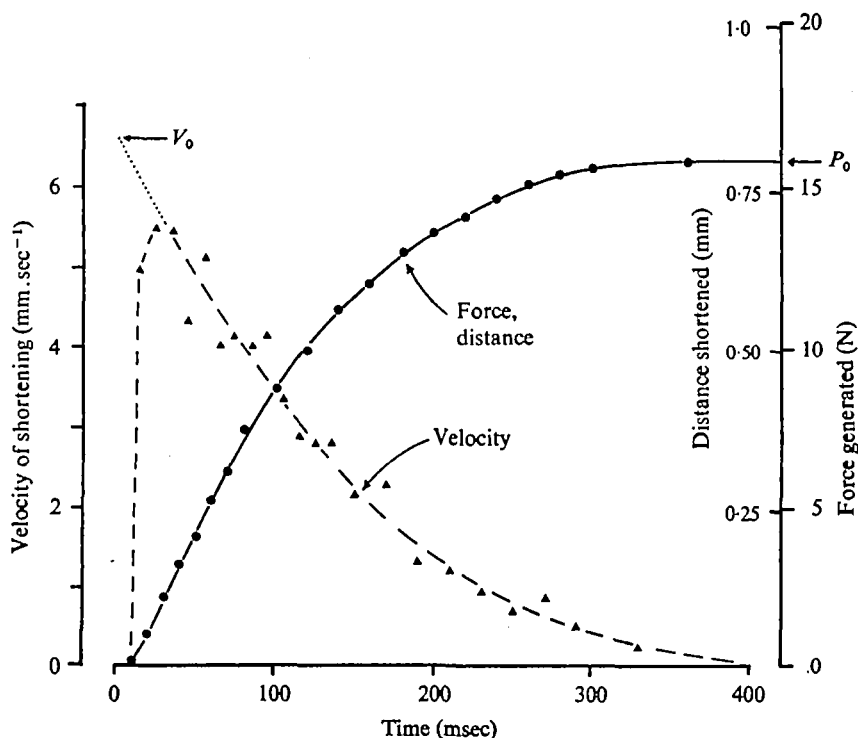
Fig. 8. Graph of force, distance and velocity against time for a locust metathoracic extensor tibiae muscle, at 30 °C, 100 stimuli.sec⁻¹ and 30° extension of the tibia. Force is obtained by calculation from the force at the distal end of the tibia, distance from the assumption that the stress–strain curve of the femoral elastic elements is linear and similar to those of Fig. 7. Velocity is obtained by differentiating the force/distance curve. V_0 is the velocity extrapolated to zero force and P_0 is the force at zero velocity.

stress. The system can be regarded as a pair of springs in series, the stronger straining 0·76 mm with a stress of 15 N and the weaker limited to a strain of 0·26 mm with a stress of, say, 7·5 N. On release, when the springs shorten, the stronger relaxes first by 0·38 mm when the stress is 7·5 N and both springs relax thereafter through a total of 1·02 mm (Fig. 7). This load line for the elastic elements of the femur assumes that the springs are linear; the semilunar processes only depart slightly from Hooke's Law but other elements in the system have unknown properties, so this is the simplest assumption. At lower stresses parallel load lines can be drawn. These load lines can be used in conjunction with the geometry of the femoro-tibial articulation to predict the forces produced from the energy stores during leg extension. This will be done in section 12.

8. *Mechanical properties of the extensor tibiae muscle*

Force/time records were obtained from over 30 legs at angles of extension of the tibia between 15 and 120°. The force measured at the distal end of the tibia was multiplied by the mechanical advantage of the articulation to give the force at the extensor apodeme. Fig. 8 is derived from such a record from the leg of a female locust at 30° extension. Force develops 10 msec after the first stimulus and rises
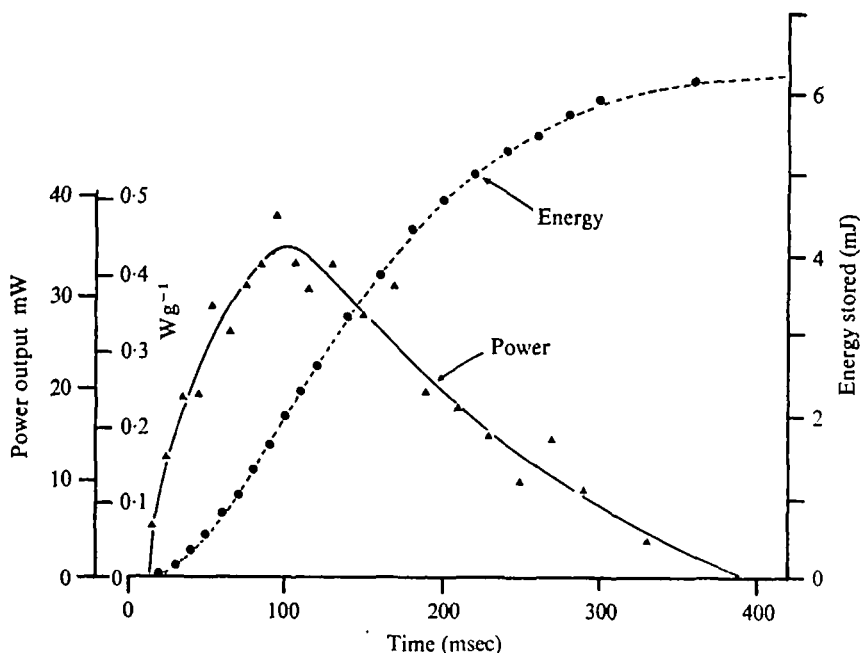
Fig. 9. Graph of power and energy production against time for locust metathoracic extensor tibiae muscle contracting at 30 °C and at 30° extension of the tibia. Power is calculated as the product of force and velocity from Fig. 8. Energy production is obtained by integrating the curve for power output.

rapidly at first, slowing to reach a maximum of 15·8 N after about 350 msec at 30 °C; at this point with this preparation the leg broke at the distal end of the femur.

The distance through which the distal part of the apodeme and the semilunar processes move with this force is 0·8 mm (Fig. 7) and, assuming a linear stress-strain relation, the strain is 50·7 μm.N^{-1}. From this the velocity of shortening at the proximal end of the apodeme can be calculated (Fig. 8). The peak velocity at 30 msec after stimulation is 5·5 mm.sec^{-1} and, extrapolated to zero time, the velocity does not exceed 7 mm.sec^{-1}.

Peak power is reached 100 msec after the start of stimulation, reaching a maximum of 36 mW (Fig. 9) at about half the peak force and velocity for the muscle. In this insect the extensor tibiae muscle weighed 80 mg, so the specific peak power output is around 0·45 W.g^{-1} (Fig. 9). The average power over the first 300 msec of contraction is 0·25 W.g^{-1}. The peak energy stored by this method is 6·3 mJ – rather less than that obtained by calculation, allowing for the non-linearity of the semilunar processes (section 4). The specific energy produced by the muscle is between 79 mJ.g^{-1} (this section) and 105 mJ.g^{-1} based on a typical muscle weight of 70 mg (section 1) and an energy storage of 7·35 mJ at a force of 15 N (section 7).

The force produced in the legs of male insects did not normally exceed 13 N, while female insects produced forces of between 12 and 16 N at from 15 to 30° extension of the tibia. These values are substantially higher than those reported elsewhere (Hoyle, 1955; Heitler, 1974) and depend on the angle of extension of the tibia and the resultant muscle fibre length.
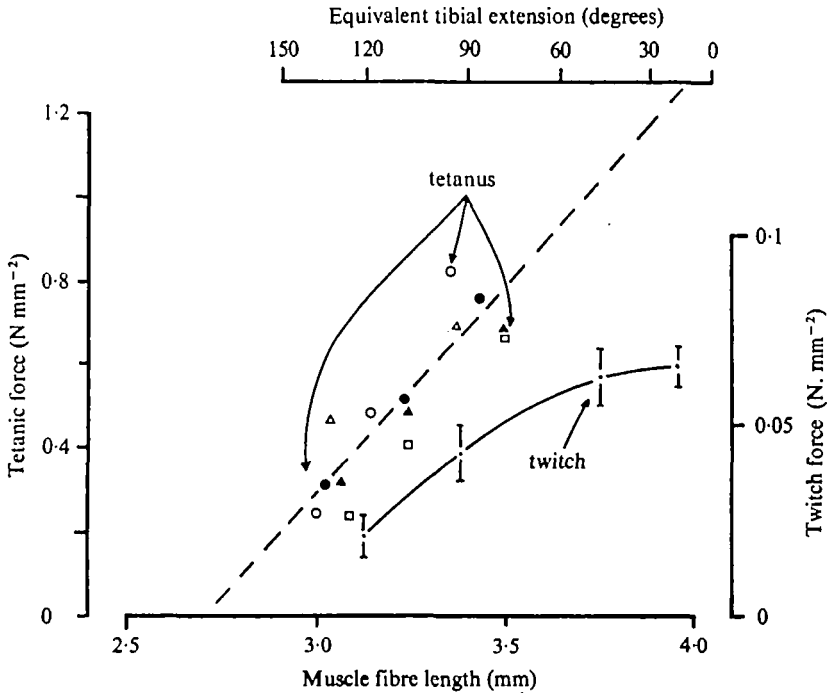
Fig. 10. Graph of the force–length relationship for locust metathoracic extensor tibiae muscle contracting at 30 °C, in tetanus at 50 stimuli/sec and for twitches produced by a single stimulus. Each symbol shows points obtained in tetanus from a single preparation at different angles of extension of the tibia, while the points and bar lines shown for twitch force are means and 95 % confidence limits for six different legs. Muscle fibre length is calculated from the force produced, the resultant strain of the cuticle and the geometry of the muscle fibres. Force is calculated from the force produced at the distal end of the tibia, the geometry of the tibio-femoral articulation and of the muscle fibres. The dashes show the linear regression of tetanic force on muscle fibre length. The equivalent tibial extension is the angle between femur and tibia if the muscle shortens and no cuticular strain occurs and if no constraints are placed on tibial extension.

An extension of the tibia from o to 30° is brought about by o·1 mm movement at the extensor apodeme (Fig. 4). A stress of 15 N causes a further direct strain of apodeme and semilunar processes of o·76 mm, a total of o·86 mm at the apodeme. The initial length of the muscle fibres is 4–4·2 mm with a femoral width of 2·65 mm, so the initial position of the apodeme insertions is, by Pythagoras, $\sqrt{(4\cdot2^2 - 1\cdot325^2)}$ or 4 mm distal to the muscle insertions on the outer wall. When strained, the apodeme moves proximad through o·86 mm to rest 3·14 mm distad of the outer insertions. Although part of the sides of the femur buckle inwards, this has little effect on most of the muscle fibres, so the fibre length becomes $\sqrt{(3\cdot14^2 + 1\cdot325^2)}$ or 3·4 mm and the angle of insertion changes from 18·5 to 24°.

With a fibre length of 3·4 mm and a muscle weight of 70 mg, the effective area of cross-section is 20·6 mm², the alternative calculation based on an apodeme area of 48 mm² and an angle of insertion of 24° gives 18·8 mm². With the worst case of a force of 12 N and an area of insertion of 20·6 mm², the force per unit cross-sectional area of fibre is 12/[20·6 (cos 24°)] N.mm⁻² or o·66 N.mm⁻², while the same sum based on 80 mg of muscle and a force of 15·8 N (this section) gives o·75 N.mm⁻².

These values are substantially higher than those found in the flight muscles of locusts, where the force is about 0·35 N.mm^{-2} at 30 °C and the A band is 3·1 μm long (Weis-Fogh, 1956) as opposed to 5·5 μm in the locust extensor tibiae (Cochrane, Elder & Usherwood, 1972).

As the leg extends, the extensor tibiae muscle fibres shorten and the angle of obliquity of the insertions increases, reducing the effective force of the muscle by the cosine of this angle. At the same time, the overlap between actin and myosin filaments will change and the force will vary accordingly (Gordon, Huxley & Julian, 1966). The relation between length and force was measured for locust extensor tibiae muscle by calculation from the force produced by standard legs at various angles of extension and from the known geometry of the muscles in the femur and of the tibio-femoral articulation. Force was measured at 30°, at 90° and at 120° extension but, as legs fatigued rapidly, the sequence was started at different extensions with different legs and results obtained after fatigue had become apparent were discarded.

The force is greatest with fibre lengths equivalent to small angles of extension of the tibia and falls away to zero at a length equivalent to an extension of about 150° (Fig. 10). The maximum force recorded in this series of experiments was around 0·8 N.mm^{-2} at 30° extension of the tibia, but in no case did the extensor apodeme or femoral cuticle fracture, as tends to occur if the stimulated leg is held fully flexed; it is probable that the experimental sarcomere length was less than that for peak force.

To test this, a series of measurements was made with single stimuli to measure the twitch force. The results are also shown in Fig. 10 and it will be seen that though the force is about one-twelfth that produced in tetanus, it is largest at fibre lengths between 3·75 and 3·95 mm. This fibre length is close to the resting length with the leg flexed. It may be inferred from this that the muscle geometry is such that maximal muscle force can never be produced in practice as the elastic elements strain beyond this point to give a fibre length at which a lower force is produced. The advantages of such a scheme are clear; the muscle can contract through a length–force condition which allows the maximum power output at a safe strain but at an isometric force which is not greatly above the safe limits of the skeleton. The maximum power output is produced at a strain of 0·3–0·5 mm and a force at the apodeme of 7–10 N (Fig. 9). At the equivalent muscle fibre length, 3·8–3·55 mm, the predicted isometric force is 1·2 N.mm^{-2}, about 1½ times that realized in practice at a fibre length of 3·4 mm (Fig. 10). The muscle produces maximum power at a force of about half the maximum reached after further shortening; at maximum power the predicted, but attainable, isometric force is 3 times the actual force, a condition described by Hill (1950).

The extensor tibiae muscle shows other adaptations which may be relevant to its function in the insect. The initial rising slope of the force–time records does not vary with different fibre lengths but, with the shortest, the maximum force is reached after 100–120 msec and, with the longest, after 300 msec. Thus, in the first few milliseconds of any contraction a similar force and power is developed at all extensions of the leg (Fig. 11).

At the end of a burst of stimulation, the muscle continues to produce force for
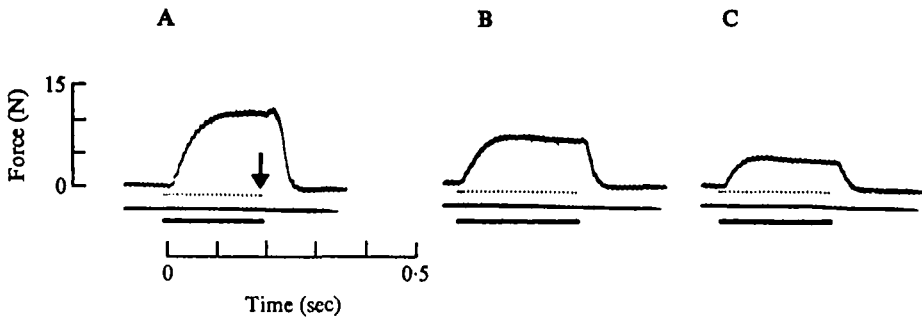
Fig. 11. Records of force against time for locust extensor tibiae muscle in tetanus at 50 stimuli/sec and at 30 °C. The upper trace shows force, the lower trace shows the stimuli, and the line below the lower trace shows the total duration of the stimulation. Records were made (A) at 30°, (B) at 90° and (C) at 120° extension of the tibia. The arrow in trace A shows an intercalated stimulus; see Fig. 12. The flexor apodeme was cut.
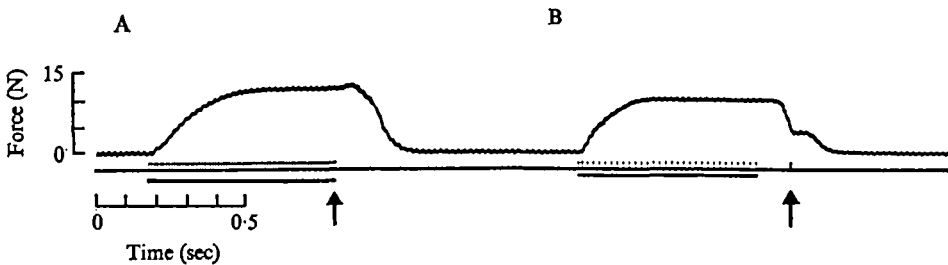

Fig. 12. As Fig. 11 but to show the effect of different types of stimulation. At A the arrow shows an intercalated stimulus, which causes the muscle force to rise and at B a single stimulus during relaxation causes the muscle to maintain its force for a further 60 msec before relaxation resumes. The flexor apodeme was cut.

a period of 40–50 msec, after which force falls away smoothly to zero 120 msec after the end of stimulation at 30 °C. Intercalated stimuli during stimulation at 25–50 stim.sec^{-1} caused the muscle to produce more force, reaching a peak some 50 msec after the stimulus (Figs. 11, 12); the muscle power output during this twitch is high, but less than that produced at lower forces. During relaxation after a burst of stimulation, a single stimulus stopped relaxation and caused the muscle to maintain the force for a further 50 msec with a latency of less than 10 msec (Fig. 12).

These effects are similar to the catch property demonstrated for this muscle by Wilson & Larrimer (1968) and it is useful to note that this muscle has a sparse sarcoplasmic reticulum (Cochrane *et al.* 1972).

The stimulation adopted in my experiments in no way reflects the pattern of excitation by the motoneurones, which appears to be very complex (Hoyle & Burrows, 1973). However, it appears that stimulation via different classes of motoneurones affects the force of the response to a greater extent than its time course (Usherwood & Grundfest, 1965), and the high forces and powers observed here suggest that the muscle is contracting near its limits.
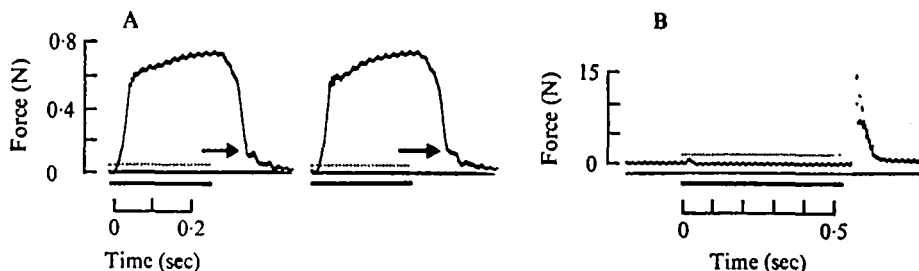
Fig. 13. Records of force against time for metafemoral muscle contracting at 30 °C.

(A) Flexor tibiae muscle in tetanus at 100 stimuli/sec; the base line of the lower, stimulus, trace acts as base line for the force trace. The arrows show the level at which the flexor catch unlocks. The extensor apodeme was cut and force was recorded with the tibia at 15° extension via a cord tied to the tibia 20 mm from the articulation with the femur; at this point the mechanical advantage of the flexor muscle is 12:1. The continuous line below the traces shows the duration of stimulation.

(B) The intact leg stimulated at 5–10° extension of the tibia. The upper, irregular, trace shows force and the lower trace shows stimuli which appear above the force trace. The continuous line at the bottom shows total duration of stimulation. There is an initial deflexion of the force trace as the leg extends slightly and then flexes fully followed by a kick lasting about 0·1 sec which occurs 50 msec after the last stimulus.

9. Mechanical properties of the flexor tibiae muscle

A maximum force of 58 mN at the force transducer, or 0·7 N at the apodeme, was recorded. The lowest force recorded from a tetanus at 50 stim.sec^{-1} was 0·45 N; these values are higher than those found by Heitler (1974), but the legs he used were smaller than those used here and my experiments were performed at 30 °C, at which temperature I have found that the force and rate of contraction are greater than at 20–25 °C.

After the start of stimulation, there is a latency of some 15 msec followed by a rise to near peak force over the next 35–40 msec; thereafter, force continues to rise slowly for over 100 msec. After stimulation ceases, force persists for about 50 msec after which force falls rapidly to reach zero 90 msec after the end of stimulation (Fig. 13A). Heitler (1974) has shown that when the force on the extensor apodeme is 16 N, the catch on the flexor apodeme disengages at a force of 0·15 N in the flexor muscle. This force is reached 37 msec after the start of stimulation and, during relaxation, about 30 msec before the muscle is completely relaxed. At this point, an inflexion in the force records is seen which is possibly due to the unlocking of the catch (arrows in Fig. 13A).

The properties of the flexor tibiae muscle are complementary to those of the extensor tibiae muscle. The force that can be produced is 3–4 times that required to prevent extension with the leg flexed, the speed with which this force is produced is far greater than that in the antagonistic extensor, and, when extension does occur, the catch ensures that the flexor is nearly completely relaxed when it is forcibly stretched by tibial extension. The relatively high strength of the flexor apodeme (section 1) is clearly adapted to this mechanical situation.

10. *Stimulation of the whole metathoracic leg*

If the intact leg is stimulated with the tibia initially flexed, tibial extension does not occur as the flexor torque exceeds the extensor torque (Brown, 1967; Heitler, 1974). When stimulation ceases, the decay of force in the flexor muscle is far more rapid than that in the extensor muscle and so the leg unlocks and the tibia kicks (Fig. 13B). The force produced in such a kick attains a maximum of 0·25 N at the distal end of the tibia or 9 N at the extensor apodeme, reaching this force in less than 10 msec after the tibia starts to move (owing to resonance in the polyester cord and the force transducer at this high rate of loading, the time course of this event cannot be defined in this experiment). Thereafter, force falls away slowly, reaching zero after about 80 msec. If such a kick is not restrained, the tibia extends by between 80 and 120°.

This 'model jump' has a feature in common with the jump of the animal. Tibial extension is far more rapid than can be accounted for by the maximum velocity of the extensor tibiae muscle when this is contracting from the resting condition. It seems unlikely that the jump results from a simultaneous motor neurone shutdown to both major femoral muscles, as both muscles maintain force for a similar period of 50 msec before starting to relax; the flexor apodeme catch will not disengage until the extensor muscle has partially relaxed, and relaxation of the extensor muscle will continue through the 25–30 msec duration of the jump impulse (section 11). From the work of Usherwood & Runion (1970) it appears that slow motor excitation of the extensor tibiae continues throughout the jump impulse.

11. *The jump impulse*

Prior to jumping, the insect flexes its metathoracic legs fully and places the first two pairs of legs symmetrically about the sagittal plane. This stance is adopted at least 150 msec before the jump. A gap can be seen between the distal end of the femur and the proximal end of the tibia and, in the last 100–200 msec, this widens as the extensor tibiae muscle contracts and the semilunar processes deflect ventrad (Fig. 5). On one occasion when the insect sat for 800 msec before jumping, an initial deflexion and strain of the semilunar processes was followed by a relaxation and a further deflexion, after which the insect jumped. This phenomenon can also be seen with constrained and freely walking insects.

In the last 20–30 msec before the jump, the hind femora, which were elevated at an angle of 30–40° above the longitudinal axis and held parallel to the sagittal plane, are depressed towards the horizontal and are swung out 15–20° either side of the sagittal axis. The animal then jumps.

The two metathoracic legs do not move in precise synchrony; one leg has been seen to depress to the substrate over a period of 1 msec followed by the other, 2–5 msec later. The first movement of the animal is detected some 3 msec after the first leg movement and thereafter the animal accelerates steadily, becoming airborne after 25–30 msec, usually by what appears to be a similar extension of both metathoracic legs.

In the six jumps filmed, the highest velocity at take-off was 3·2 m.sec⁻¹, which is
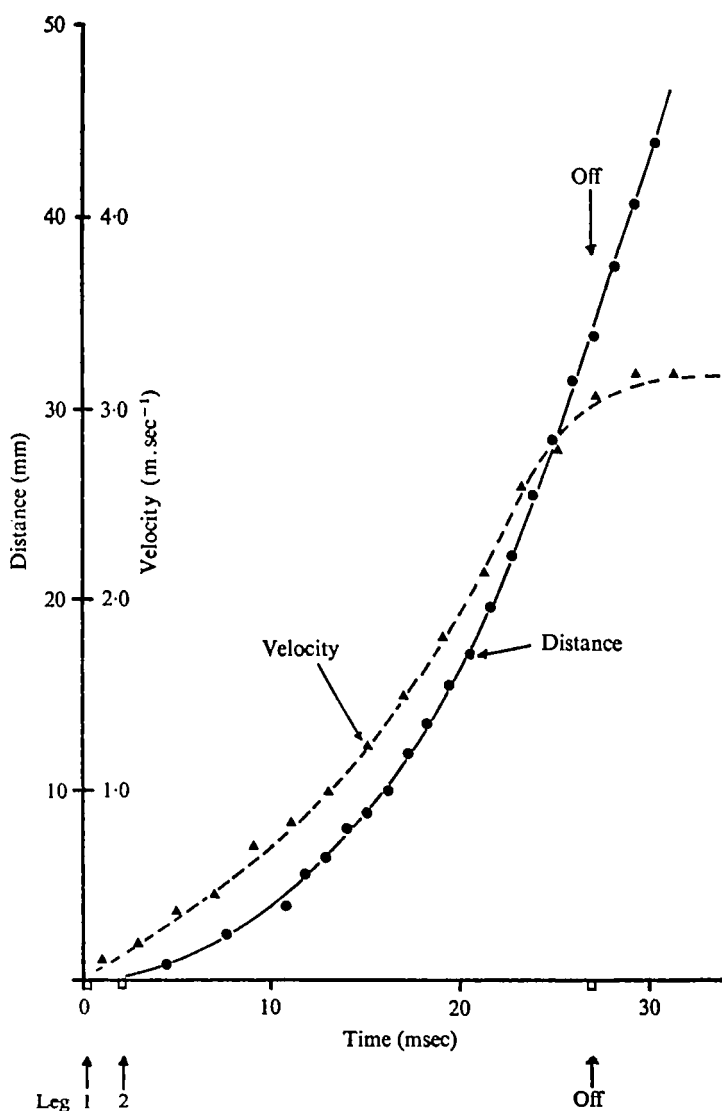
Fig. 14. Graph of distance and velocity against time for a 1·7 g jumping male locust. Distance was obtained from tracings from individual frames of a 930 frame/sec film, starting from the first detectable leg movement. The arrows on the abscissa show when the two metathoracic legs unlocked and when the animal left the ground.

slightly below the maximum performance of a male insect (section 2). The energy of this impulse is given by

$$E = \frac{m \cdot V^2}{2}, \tag{12}$$

which with the 1·7 g male insect gives 8·65 mJ, 4·3 mJ per leg.

Distance was plotted against time (Fig. 14) and, from this, velocity against time was derived by differentiation. Angular velocity of the tibia with respect to its initial

position was also recorded; the maximum was 9° in 1 frame – about 8500° sec⁻¹ or 150 rad.sec⁻¹.

In two jumps the insect jumped using one leg and released the other when fully airborne. From this it was possible to plot angular position and angular velocity against time for the unloaded tibia (Fig. 15). The movement takes the form of a highly damped oscillation which dies out by the 3rd cycle with a frequency of oscillation of 130–140 Hz. The maximum angular velocity is 800 rad.sec⁻¹ and from this it is possible to calculate the energy of rotation of the tibia.

Following Taylor (1963), the energy of rotation is given by

$$E = \frac{m}{12}(l^2 + d^2)\frac{\omega^2}{2},$$ (13)

where m is the mass of the tibia and tarsus, 24 mg, l is the length of the tibia and tarsus, 30 mm, d is the diameter of the tibia, *ca*. 1·5 mm (but this term can be neglected) and ω is the angular velocity, 800 rad.sec⁻¹. The energy of rotation is calculated as 0·58 mJ. It seems likely that the rotation of the femur in the opposite direction has a similar energy and so the total energy is about 1·16 mJ. The jump of the 1·7 g locust in which this event was filmed attained a maximum velocity of 1·5 m.sec⁻¹ and thus the other leg produced an energy of 1·91 mJ. This larger figure can be accounted for, in part, by the lower rate of leg extension and hence lower energy losses in the cuticle and from the viscosity of the muscles. These losses can be calculated by consideration of the amplitude of successive cycles of the vibration (Dent & Akhurst, 1969).

The loss factor, ξ, is given by

$$\log_e \frac{X_0}{X_1} = \frac{2\pi.\xi}{\sqrt{(1 - \xi^2)}},$$ (14)

where X_0 is the initial amplitude, X_1 is the amplitude after one cycle and 2π is the angular rotation in radians. With the oscillation of the tibia, there is the problem of defining the centre of oscillation; I have taken the positions of maximum angular velocity in either direction. There is a slow extension of 30° in 20 msec superimposed on the 130 Hz oscillation of the tibia (Fig. 15), and in calculating the loss factor this shifting centre line has been used as a datum.

The loss factor has been calculated for the first four half-cycles of the kick (Fig. 15). As the centre of oscillation is hardest to define in the first half-cycle, the value for the loss factor, which is small, is imprecise but increases steadily in succeeding half cycles. This is possibly due to steadily increasing damping by the extensor tibiae after release of the stored energy and to the change from a state of almost complete relaxation to one of generating tension.

The energy loss from damping can be most simply estimated by measurement of the amplitude of successive half-cycles. The power is proportional to the square of the amplitude and so the relative energy loss is $1 - (X_1^2/X_0^2)$. For the first half-cycle of the kick this loss is 20–30 %. This is similar to the differences between the energy of rotation of the leg and the energy of the jump.

In a normal jump, extension is most rapid in the last 15 msec; this rotation can be related to that occurring in an unrestrained kick (Fig. 15). The jump rotation
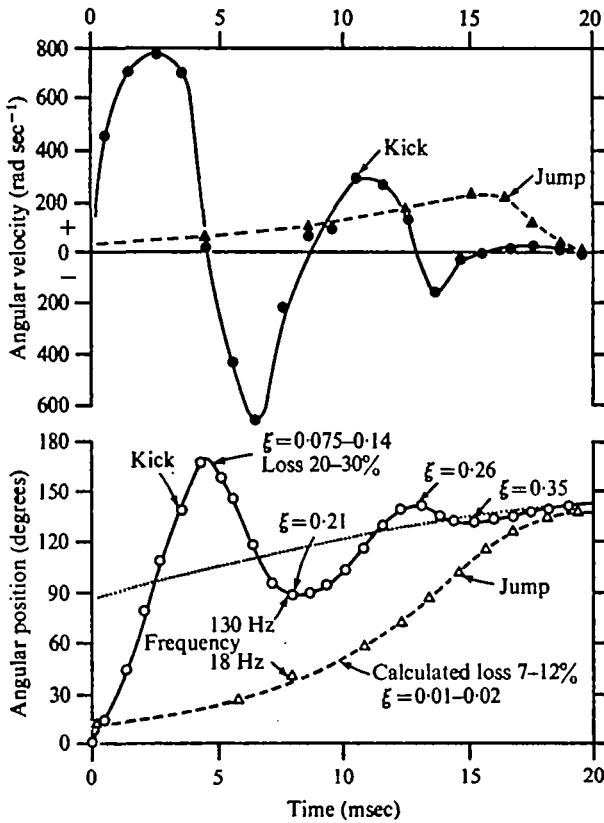
Fig. 15. Graphs of angular position and angular velocity against time for leg extension during a locust jump and for a kick by an unloaded tibia obtained from high-speed films. In the jump, the angular position and velocity are of the tibia with respect to the femur; the angular velocity of each is half that indicated in the upper graph. In the case of the kick, there is only a small amplitude of rotation of the femur. This is hard to measure and so angular rotation and velocity are shown for the tibia alone. The dotted line shows the probable centre of oscillation during the kick. The energy loss and the loss factor, ξ, have been calculated and are shown for both lines.

appears as a quarter-cycle of frequency approximately 18 Hz or about 0·14 that in the kick. If the loss is viscous, the loss factor will be proportional to the frequency and so in the jump will be 0·14 that during the kick.

The energy loss due to damping during the jump can be estimated only if several assumptions are made; firstly, that the rotation during the jump can be regarded as harmonic but over a small part of a cycle, secondly, that the losses will be related to those in the similar initial part of the kick. In this, it is necessary to estimate the notional amplitude of the vibration after a quarter of a half-cycle. Where the loss factor is known, this will be either $e^{-\xi\pi/2}$ or $e^{-\xi\pi}$ times the original amplitude, and the relative power will be the square of this ratio. Treating the jump as a half-cycle with a loss factor of 0·02, the worst case, the energy loss is 12 %. In the best case, a quarter-cycle with a loss factor of 0·01, the energy loss is 3 %. Such energy losses, though not insignificant, do not upset the energy budget proposed earlier. The energy of rotation of the tibia is not available for jumping. Since the femur is
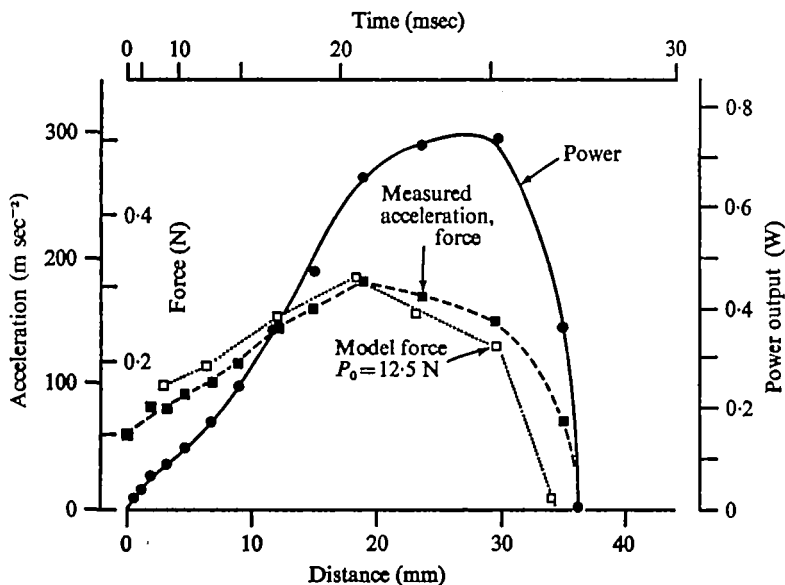
Fig. 16. Graph of force, acceleration and power against distance and time for the jump of Fig. 14. Acceleration is the differential of velocity from Fig. 14, and is converted to force by multiplication by the animal's mass. Power is the product of force (this figure) and velocity (Fig. 14). The Model Force curve is calculated as that produced by a spring with the properties of the 12·5 N load line of Fig. 7 relaxing into a lever system with the properties of the metathoracic leg shown in Fig. 4.

depressed as the tibia extends, the angular velocity of the rotation of the tibia about its centre will be half that shown in Fig. 15 or 150 rad.sec^{-1} and the energy of rotation (formula 13) will be 0·02 mJ, which is negligible. The femur also attains this angular velocity and, treating it as a cylinder of mass 120 mg, of diameter 4 mm and length 25 mm, the energy of rotation is 0·07 mJ, which can probably be provided directly by the coxal muscles.

During the jump the initial acceleration of 60 m.sec^{-2} rises after 21 msec to a maximum of 180 m.sec^{-2} and then falls as the animal approaches full leg extension (Fig. 16). Over the central 20 mm of extension, the force is fairly constant. Power is obtained as the product of force and velocity; the peak output is 0·74 W at close to maximum velocity and maximum acceleration.

As the maximum power output of each extensor tibiae muscle is 36 mW (section 8) the power amplification resulting from energy storage is about 10-fold. At the maximum velocity of shortening of the extensor tibiae muscle (7 mm.sec^{-1}) the velocity of tibial extension would be 0·14 m.sec^{-1} at 90° extension, which is about one-twentieth that achieved in a jump. It appears from this that direct action of the extensor tibiae muscle is not possible after the first 3 mm of the jump and that the effect of direct muscle action is negligible.

12. *A model of the mechanism*

It has been shown that the elastic elements can be regarded as a two-part spring (section 7) which strains at a rate dependent on the stress (Fig. 7). The components of this spring, the semilunar processes and the extensor apodeme, on relaxation, act

either side of the femoro-tibial articulation and through the contracted extensor tibiae muscle. The force that is produced during tibial extension can be calculated by consideration of the mechanical advantage of the articulation (Fig. 4) and the properties of the relaxing spring (Fig. 7). This treatment produces a family of force–distance curves depending on the initial stress in the elastic elements, one of which (Fig. 16) corresponds closely to the force distance curve calculated for the jump of Fig. 14 and requires an initial stress in the elastic elements of 12·5 N, which is within the observed capabilities of the extensor tibiae muscle. Similar curves have been fitted to the other jumps measured and do not require more than minor modifications to the stress–strain curves of Fig. 7.

13. *Other Orthoptera*

All Acridioids that I have examined display the principal anatomical features described here in the locust, so it seems likely that the mechanism of jumping differs only in detail. In Grylloids, the metathoracic leg is more robust and works at a lower mechanical advantage. Although many Grylloids run and dig actively, they jump poorly. The semilunar process in *Gryllus* is less developed than in *Schistocerca*, and the leg appears to be less specialized for jumping.

In Tettigonioids the metathoracic legs are usually very long, and both the distal end of the femur and the tibia are thin. Some of these long-horned grasshoppers jump well but the mechanism shows a different mechanical arrangement to that in Acridioids. The mechanical advantage of the tibio-femoral articulation is even higher than in locusts and the shape of the femur is different. In *Ephippiger* or *Tettigonia* the femur is shaped like a very long-necked bottle with the muscle concentrated in the proximal expanded region and a long thin extensor apodeme passing through the long thin neck of the distal part of the femur. At the articulation of the tibia, the cuticle is sclerotized but does not show the specialized bow-like semilunar processes of the locust nor does the articulation distort in the same way. It appears that energy can be stored, but mostly in the extensor apodeme, which is even more specialized than in Acridioids, with possible minor strains occurring by compression of the outer walls of the femur and distortion of the unspecialized femoro-tibial articulation.

While the system found in Tettigonioids is perfectly feasible, its exploitation requires high mechanical advantages to utilize the small strains that occur in the apodeme, and, because of structural limitations at the articulations, lower forces and longer legs are advantageous.

DISCUSSION

Energy storage in a small jumping animal is advantageous. There is a considerable power amplification, and hence velocity amplification, on release. This is achieved at a small weight penalty using passive skeletal elements; in the locust the stores weigh under 4 mg per leg and store the energy of 70 mg of muscle. In addition, by suitable geometry of the femoro-tibial articulation, it is possible to achieve an almost constant acceleration during the impulse, with a steadily rising power output from the energy stores.

The force–velocity relation of muscle is such that as velocity rises, force falls, and

hence power, which is the product of force and velocity, is maximal at about one-third the isometric force and one-third the unloaded velocity (Hill, 1938, 1950). To achieve a constant force from direct muscular activity, the system must contract from the isometric condition to the condition of maximum power which, in a small animal, implies a very rapid contraction.

Contraction at maximum power occurs at one-third maximum force. The energy is thus one-third that of the same contraction at just below isometric force and represents an uneconomic use of the muscle. If the muscle can be arranged to contract at a biologically acceptable rate into an energy store, attaining its isometric tension, the energy that can be stored will be around one-half the maximum energy of a single slow contraction (formula 10) and hence 1·5 times that of the contraction at maximum power. This is achieved at a 5 % weight penalty in storing the energy. Various features of the locust extensor tibiae muscle are adapted to this function. While the contraction is quite slow, the power output is high; the peak value of 0·45 W.g^{-1} may be compared with a value of 0·86 W.g^{-1} for pigeon flight-muscle (Pennycuick & Parker, 1966) and a mean value for locust flight muscle of 0·19 W.g^{-1} (Neville, 1965). This, in a slow contraction, is achieved by producing a high force, and if the overall range of contraction is similar the energy of the single contraction will be greater.

Insects show considerable plasticity in their use of muscle, and within the locust there is adaptation both of the excitation–contraction coupling system and of the sarcomere length to the varying mechanical tasks performed by the muscles (e.g. Weis Fogh, 1956; Neville, 1965; Cochrane *et al.* 1972).

Insects also use various types of energy stores which appear to have been modified for the purpose of jumping from structures involved in other aspects of locomotion. Thus the flea uses a resilin store situated between the pleuron and tergum of the metathorax (Bennet-Clark & Lucey, 1967) which is derived from the elastic wing-hinge ligaments of the pterothorax and which originally was used as a buffer to minimize inertial losses in flight (see Weis-Fogh, 1961; Jensen & Weis-Fogh, 1962). As an energy store for the jump of a small insect, resilin has the useful properties of high energy storage and rapid energy release but, from the low Young's Modulus, it is most appropriately used in shear or in short thick structures (Bennet-Clark, 1975). The use of conventional cuticle as an energy store requires a different design approach. Conventional cuticle has a high Young's modulus and the elastic elongation is only a few per cent. As a result, it is appropriate to use the material for stores in the form of bending beams or long thin springs in tension and, even so, the strains are very small (which is doubtless why they have escaped notice). To exploit such stores, the mechanical advantage of the extending leg system must be high and the forces produced must approach the tensile limits of the structures; all this is seen in the locust metathoracic leg.

It is possible that energy is stored in series elastic elements of the contracted muscle (Usherwood & Runion, 1970). While it is not possible to reject this, the evidence presented here suggests that, at best, elastic elements in the muscles play a minor part in the energy budget and, at worst, are negligible and unimportant. In fleas, where several genera have been examined, there is a good circumstantial relationship between the size of the resilin store and the observed jumping performance (Bennet-Clark & Lucey, 1967).

6

All insect jumping mechanisms appear to have a catch to prevent extension during energy storage; this is seen in fleas (Bennet-Clark & Lucey, 1967), in click beetles (Evans, 1972) and in locusts (Heitler, 1974), and this appears to have two different functions. Firstly and obviously, it allows substantial quantities of energy to be stored. Secondly, such a catch allows the antagonistic flexor or catch-engaging system to be partly or fully relaxed so that when the stored energy is released the antagonist is not damaged; it should be noted that locusts with Heitler's (1974) catch made inoperative will still jump although less well, and that in the kick of Fig. 15, the flexor tibiae muscle was elongated at 1·2 m.sec^{-1} or about 100 lengths/sec. In a normal jump the velocity can be as high as 30 lengths/sec, which is outside the normal range of muscular shortening and relaxation, so an unacceptable proportion of the stored energy may be dissipated if the flexor muscle is not relaxed.

By contrast, jumping mammals do not appear to use catch mechanisms during energy storage although it is clear that energy in both standing and running jumps is stored in tendons (Alexander, 1974; Bennet-Clark, 1975). As mammals are larger than insects, the difference between the period of storage and the period of the impulse is less marked and the time for flexor, or antagonist relaxation is acceptably long. Although it is clear that energy storage in mammals is important (e.g. Camp & Smith, 1942), the energetics has been largely neglected.

A further advantage of energy storage exists for a poikilotherm. At low temperatures the velocity of contraction of muscles is low but the force can still be fairly high. Walking and the rate of energy storage may be slow but the power produced during a jump will be far less affected; this can be seen in both fleas (Bennet-Clark & Lucey, 1967) and grasshoppers.

The jump of the locust may be contrasted with that of the click beetle, *Athous* (Evans, 1973). In both, energy is stored by contraction at high power and to a high force by a muscle which also transmits the force during the impulse. In *Athous*, the distance over which the impulse is given is under 2 mm and the power amplification is about 1000 times. A large part of the energy appears in the kinetic energy of rotation of the prothorax and posterior part of the body which continue to vibrate when the animal is airborne; the energy involved is about 40% of the total energy stored. In the locust the impulse is given over about 35 mm and the power amplification is only 10-fold. The accelerations and forces are relatively lower and the energy loss in rotating the tibia is less than 1% of the energy used in jumping. It is clearly advantageous to extend a long light structure and this condition is usual in jumping animals.

It has been no part of the present study to examine the neuro-muscular events associated with jumping, and it is not suggested that the patterns of stimulation used in my experiments produce the optimal muscle performance or reflect those produced by the animal. The animal appears to be able to control the force developed in the extensor tibiae muscle to two ends: control of the distance jumped and avoidance of damage to the skeleton. The study of these aspects would be of considerable interest.

It is a great pleasure to record, once again, my gratitude to Eric Lucey for his skill in making films of jumping locusts and for allowing me to make use of facilities

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