

THE JUMPING MECHANISM OF SALTICID SPIDERS

BY D. A. PARRY AND R. H. J. BROWN

Zoological Laboratory, Cambridge

(Received 13 June 1959)

(With Plates 13 and 14)

INTRODUCTION

There are no extensor muscles at the 'hinge joints' (femur-patella and tibia-basitarsus joints) of the spider leg. Parry & Brown (1959) have recently produced evidence that at these joints extension is due to the haemocoelic blood pressure in the leg: we measured this pressure, established an empirical relation between pressure and torque at the hinge joints, and used this relation to show that the observed pressures are adequate to account for the torques developed by the living spider.

In this paper we consider whether a hydraulic mechanism is likely to account for the jump of the jumping spider *Sitticus pubescens* (Fabricius: Salticidae). First a description of the jump is given and it is shown to depend almost entirely on the sudden straightening of the fourth pair of legs. From photographs of the jump we estimate the mean acceleration during take-off and hence the propulsive force and the torques at the hinge joints. Finally we use the relation between torque and blood pressure already established for the house spider *Tegenaria* sp. (Parry & Brown, 1959) to obtain a rough estimate of the blood pressures which would be needed to account for the jump.

DESCRIPTION OF THE JUMP

Method

The photographic equipment consists of a continuously-running camera synchronized with a British Thomson-Houston Type FAI discharge tube used as a multiple-flash light source (Brown & Popple, 1955). The spider is photographed while jumping across a gap of about 5 cm. from a narrow take-off platform to a wider landing platform. By idling the camera motor and then suddenly releasing the clutch when the spider is judged to be on the point of jumping, we were able to get a number of sequences of the jump taken at maximum camera speed—167 half-frames/sec. (6 msec. per half-frame) on 35 mm. film. In addition to these sequences we also took a number of multiple-image photographs of the complete jump, using a flash interval of 7 msec. and a 'black box' background. All this work was done at a temperature of about 20° C.

The jump

Unlike, for example, most jumping insects, the salticid spiders lack any obvious specialization of their legs and the way in which they jump does not seem to have

been determined. The jump of a mature male *Sitticus pubescens* is shown in Pl. 13, and the following points will be noted: (a) The fourth legs are held in a plane parallel to the vertical sagittal plane of the animal and straighten to their full length during the jump chiefly owing to extension at the femur-patella hinge joint and to depression of the femur; (b) the third legs are held laterally and move through a small angle before losing contact with the ground; (c) the first and second legs are held off the ground and do not contribute to the jump.

The multiple-image photographs (Pl. 14) show the use to which the drag-line silk is put during the jump. In Pl. 14a the animal executes a rather flat trajectory, drawing out a silk thread behind it (visible in the first two images and also bridging the gap at the end of the jump). Tension in this thread probably accounts for the reversal, in mid-air, of the animal's initial counter-clockwise rotation (pitch). In Pl. 14b there is a similar initial rotation, but here the tension in the thread appears to have suddenly increased so that not only is the rotation reversed but the animal drops almost vertically at the end of its jump. In Pl. 14c the thread seems to have broken and the animal makes a complete somersault.

It must be emphasized that the description just given of the salticid jump applies to *Sitticus pubescens* alone and that other species may jump differently, although we have no reason to believe that there are radical differences. For instance the zebra spider *Salticus scenicus* (Clerck) uses both the third and fourth pairs of legs when jumping, the third pair leaving the ground after the fourth pair. It is particularly fortunate for our purposes that in the species we happened to choose for study the jump is almost entirely due to a single pair of legs: otherwise the torques at the joints could not have been resolved.

TORQUES AT THE LEG JOINTS

Method

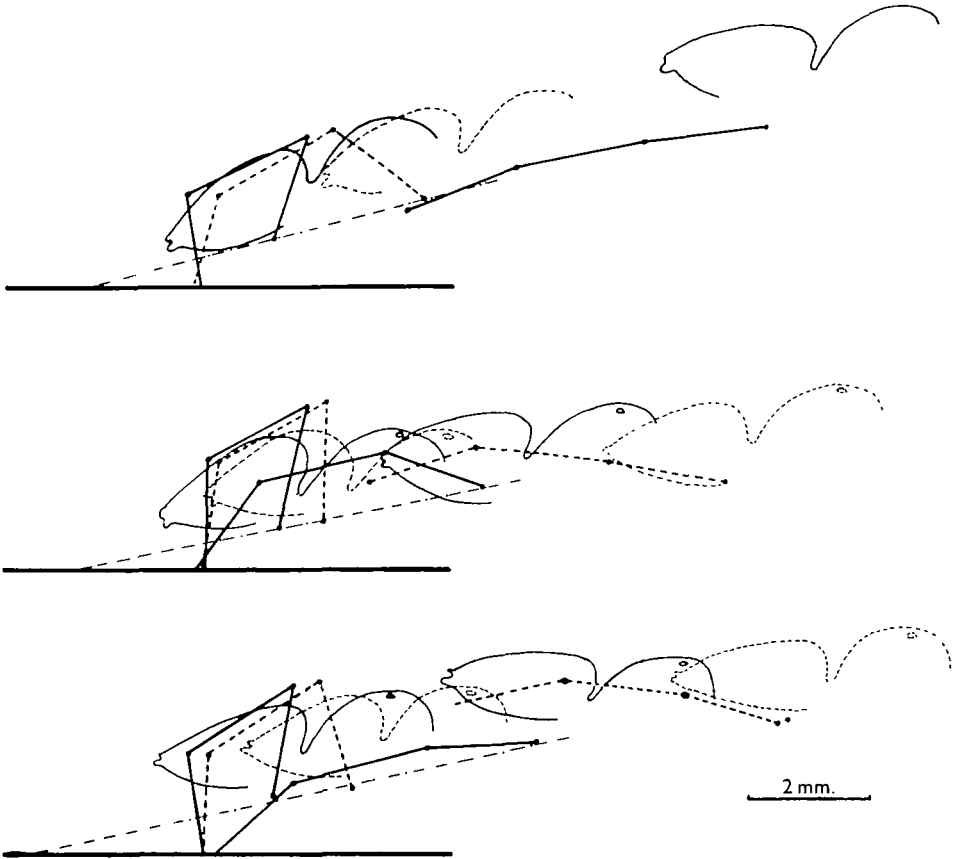
Details of the method used in calculating the torques at the leg joints during the jump are given in the appendix. In principle the method is as follows. From a photographic sequence we measure the angle of take-off, the distance moved by the spider's body during take-off, and the velocity of take-off. Thus we obtain the mean acceleration and, knowing the spider's mass, the magnitude and direction of the force acting on the spider. Taking this force to be equally distributed between the feet of the fourth pair of legs, we then calculate the torques at the joints for each of the leg configurations shown in the film.

The principal assumptions made in this calculation are:

(a) The third pair of legs contribute a negligible amount to the jump (the first and second legs need not be considered because they are held off the ground). This assumption is supported by the fact that removal of the third pair of legs has little effect on the take-off velocity of the jump—see 'other measurements of take-off velocity' below.

(b) The animal accelerates uniformly in a straight line. That the take-off path is roughly straight may be seen from the tracings of three jumps shown in Text-fig. 1. Whether the acceleration is uniform cannot be determined without a greatly

increased flash frequency and camera speed. This is one reason why our numerical results must be taken as approximate. They should, however, be adequate to show whether active extension is occurring at the hinge joints, and whether it would be reasonable to account for this extension in terms of blood pressure.



Text-fig. 1. Tracings of three jumps. The disposition of the fourth leg is shown as far as the trochanter-femur joint.

Results

Text-fig. 2 contains an analysis of eight jumps of two different spiders, each diagram showing the disposition of the near fourth leg in the two or three frames (6 msec. intervals) occupied by the jump. In each case the first leg position is the one found immediately before movement begins. The torques present at each hinge joint and at the trochanter-femur joint are shown on the diagrams (unbracketed bold figures), the units being dyne-cm. The following convention is observed in regard to sign: torques *not underlined* act clockwise on the more distal segment; torques *underlined* act anti-clockwise on the more distal segment. It will be seen that the torques at the two hinge joints are always such as to produce extension at these joints; whereas those acting on the femur tend to produce elevation at first

but may change to a depression towards the end of the jump. Except when the legs are almost outstretched the torques at the hinge joints are considerably larger than those at the base of the leg, the latter always being relatively small.

PRESSURE IN THE LEG

We have shown (Parry & Brown, 1959) that under static conditions the following relation between torque (C) and pressure (P) holds good for the *Tegenaria* hinge joint:

$$C = k_{\theta} \times P,$$

where k_{θ} is a constant for any given joint angle. If C is measured in dyne-cm. and P is measured in dynes/cm.² then k_{θ} has the dimension cm.³ and is numerically equal to $\Delta v/\Delta \theta$ or the rate of change of joint volume with angle. It thus depends only on the geometry of the joint and for similar joints—such as the *Tegenaria* and salticid hinge joints—will vary with the cube of the linear dimension. Table 1 shows, for each hinge joint, first the values of k_{θ} for *Tegenaria* (Parry & Brown, 1959), and then the calculated values of k_{θ} for the two salticids used in our experiments, obtained by multiplying the *Tegenaria* values by the ratio of the cubes of the respective hinge lengths. The actual lengths of the hinges were as follows. Upper joint: *Tegenaria*: 0.830 mm.; salticid *A*: 0.247 mm.; salticid *B*: 0.304 mm. Lower joint: *Tegenaria*: 0.600 mm.; salticid *A*: 0.160 mm.; salticid *B*: 0.198 mm.

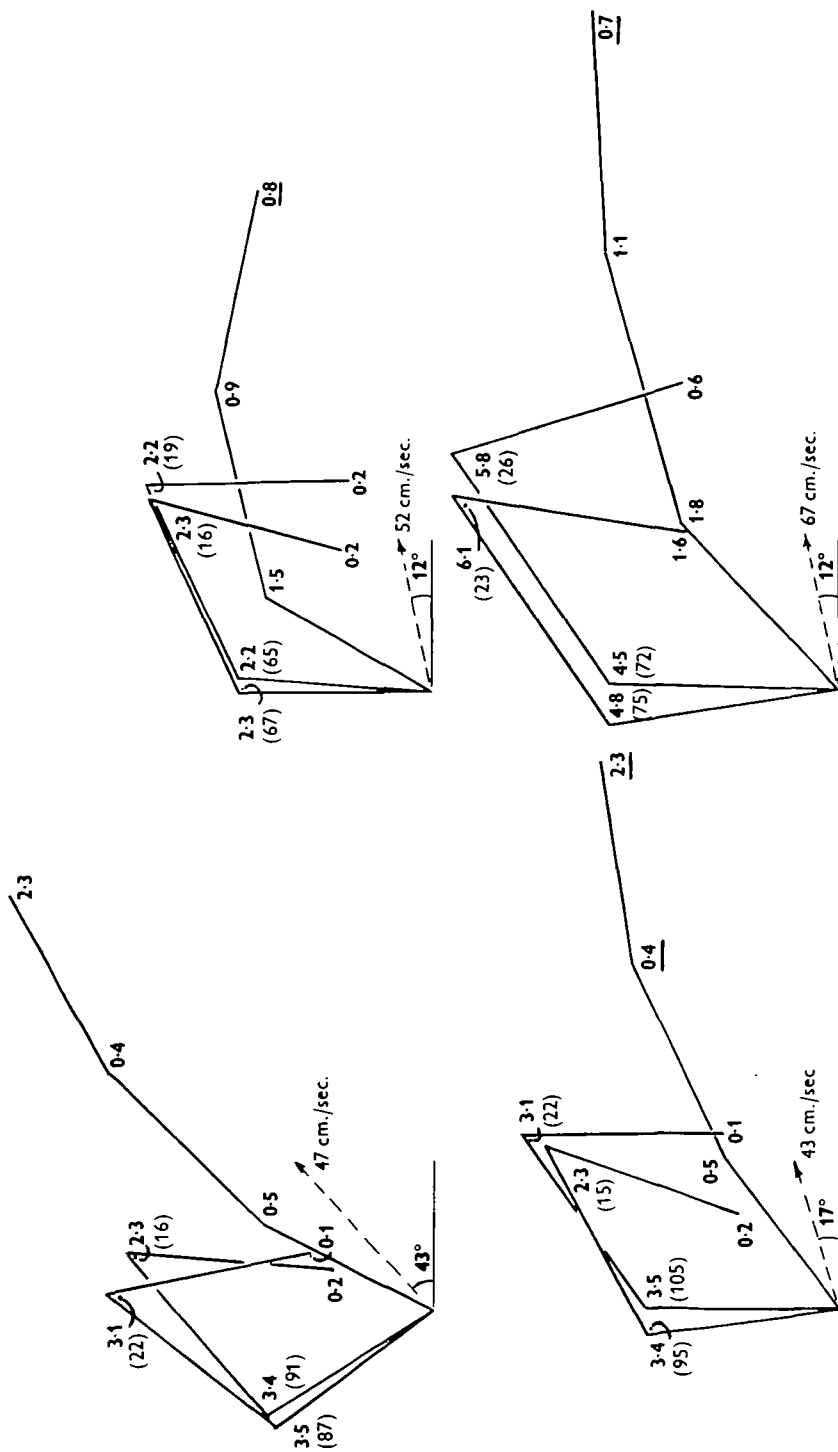
Table 1

Joint angle	40°	60°	80°	100°	120°	140°	160°
Upper joint							
<i>Tegenaria</i>	440	370	320	310	300	290	$200 \times 10^{-3} \text{ mm.}^3 = k_{\theta}$
<i>Sitticus</i> , spider <i>A</i>	11	10	8	8	8	8	5
<i>Sitticus</i> , spider <i>B</i>	22	18	16	15	15	14	10
Lower joint							
<i>Tegenaria</i>	—	—	170	150	130	130	$120 \times 10^{-3} \text{ mm.}^3 = k_{\theta}$
<i>Sitticus</i> , spider <i>A</i>	—	—	3	3	3	3	2
<i>Sitticus</i> , spider <i>B</i>	—	—	6	5	5	5	4

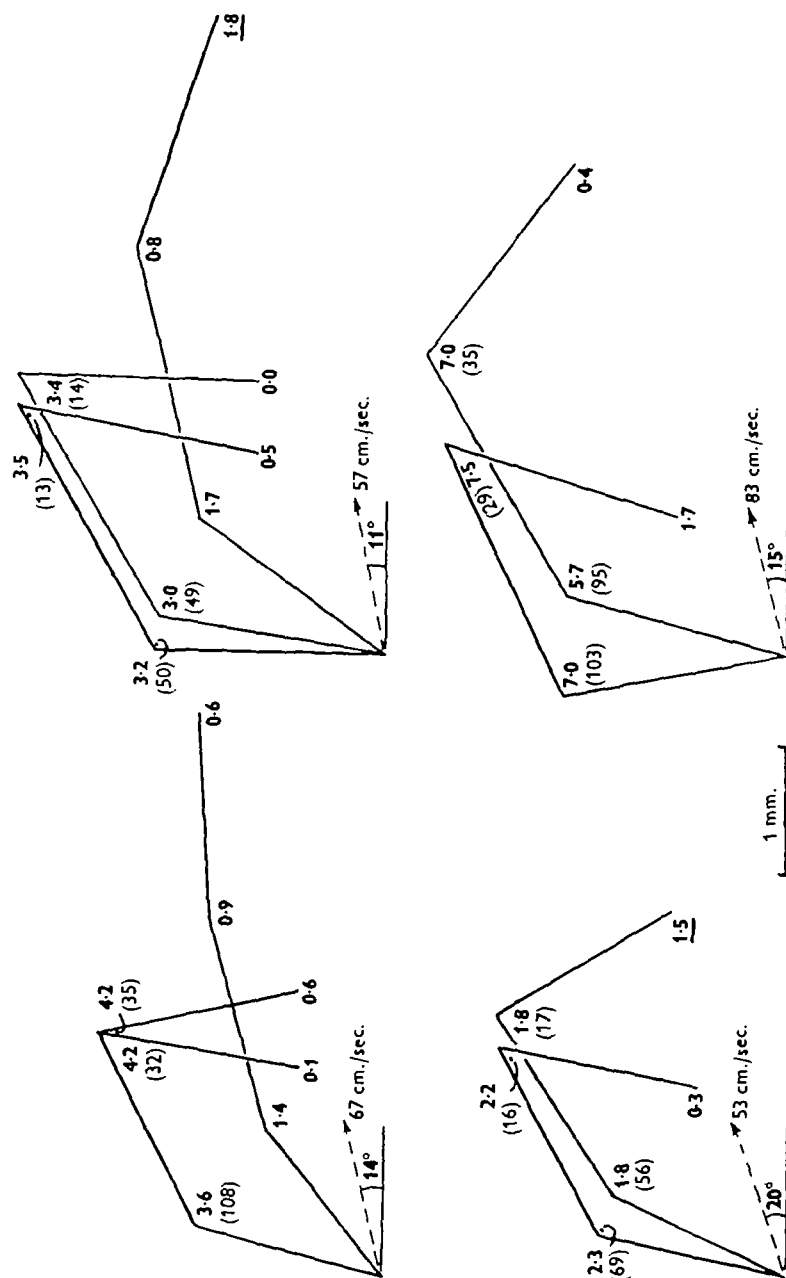
We have used these calculated values of k_{θ} to estimate the pressures needed to produce the torques developed during the jump—the pressure in cm. Hg is shown in parentheses in Text-fig. 2 beside the corresponding torques. It will be noted that:

(a) Although the torques are about the same at the two hinge joints, the corresponding pressures appear to be greater at the lower joint owing to its smaller size. In fact, unless viscosity effects are important, the pressure must be the same throughout the leg and the apparently lower pressure at the upper joint must therefore be due to flexor muscle tension.

(b) The absolute values of the calculated pressures can only be expected to indicate an order of magnitude because they are based on estimates of the torques and on the cube of a ratio of dimensions. Thus an error of 10% in the ratio of the



Text-fig. 2. For legend see p. 659.



Text-fig. 2. Tracings of the fourth leg up to the trochanter-femur joint during eight jumps. Unbracketed bold figures are torques in dyne-cm. (undefined figures indicate that the torque acts anti-clockwise on the more distal segment). Figures in parentheses are calculated pressures in cm. Hg. These are not shown when k_0 is small and changing rapidly—i.e. when the joint is becoming fully extended.

hinge lengths would produce an error of 25 % in the calculated pressures. In fact some of the pressures at the lower hinge joint are improbably high, but all lie within a factor of two and a half of the peak pressures actually measured in the leg of *Tegenaria* (Parry & Brown, 1959). Our results are therefore compatible with the idea that the hinge-joint torques are due to hydraulic pressure. It should be noted that, between similar animals of different size, the pressures will be similar because the force of a muscle is proportional to its cross-section—i.e. Force/Area (\propto pressure) is constant.

Direct evidence that the blood pressure increases during jumping is provided by the behaviour of the leg spines which, in many spiders, become erect when pressure is applied to the body or to an isolated leg. Pl. 13 shows the spines erecting on the legs during the jump—this is clearly seen on the first and fourth legs and is also visible on the third legs (compare the first three sequences). The fact that erection is not limited to the jumping legs strongly supports the idea that the increase in pressure occurs throughout the prosoma.

OTHER MEASUREMENTS OF TAKE-OFF VELOCITY

Two other methods are available for measuring the take-off velocity and angle of take-off. These do not give the take-off distance and so the acceleration and force cannot be calculated; they do, however, provide an independent indication of the spiders' normal performance. These methods are:

(a) The spider is allowed to jump across a parallel beam of light so that its shadow falls on a sheet of graph paper. One observer notes the maximum height of the trajectory of the shadow while another observer notes the range and the height of the landing point above or below the take-off point. These measurements define the trajectory and enable the velocity of take-off and the angle of elevation to be calculated.

(b) From multiple-image photographs (e.g. Pl. 14) the angle of take-off and the maximum height can be measured: these parameters determine the velocity.

Estimations of the take-off velocity obtained by these two methods are shown in Table 2.

Table 2

	No. of observations	Mean velocity (cm./sec.)
Method (a)		
Spider <i>A</i>	25	79 \pm 8
Spider <i>A</i> with 3rd legs removed	8	64 \pm 6
Spider <i>B</i>	13	76 \pm 9
Method (b)		
Spider <i>A</i>	12	75 \pm 8

DISCUSSION

We have shown that when jumping *Sitticus pubescens* suddenly extends its fourth pair of legs, which contribute almost all the motive force. Two of the joints involved are hinge joints and lack extensor muscles, and yet we estimate that the extension

torques at these joints are considerable. Perhaps the most significant evidence that extension at the hinge joints is due to hydraulic forces comes from the unexpected discovery that the leg spines become erect during the jump—a result of increased body pressure which can be demonstrated on many spiders. Calculation of the actual pressures at the joints needed to produce the estimated torques can only be very approximate. They do, however, fall within a factor of about two of the peak pressures actually measured in the *Tegenaria* leg (Parry & Brown, 1959).

Although we have thus produced evidence that the jump is due to hydraulic forces, we are still far from understanding the detailed mechanism involved. Some of the main points yet to be decided are:

(a) Which muscles control the blood pressure? We believe they are in the prosoma—see Parry & Brown (1959) and also note that spine erection is not limited to the jumping legs.

(b) Do the muscles shorten during the jump; or do they do so before the jump begins, the work being stored as elastic energy?

(c) What pressure gradients occur within the leg due to the flow of blood into the expanding hinge joints?

We hope that further studies of larger spiders may throw more light on some of these questions.

The range of a projectile depends on the angle of projection and the square of the initial ('take-off') velocity $\{R = \sin 2\theta \times (v^2/g)\}$ and for a given terminal velocity is greatest when $\theta = 45^\circ$. Usually *Sitticus pubescens* takes off at an angle less than 45° and in most of our determinations of take-off velocity it landed on a vertical surface placed up to 7 cm. away. The greatest take-off velocity encountered was 99 cm./sec., and if the angle had been 45° this would have produced a jump of 10 cm. provided there was no check from the drag-line. Energy considerations show that, *other things being equal*, range should be independent of size:

Range $\propto v^2$ (see above).

Work done by muscles $\approx \frac{1}{2}mv^2$ (neglecting increase in potential energy during take-off which is relatively small).

Therefore range $\propto \frac{\text{work done by muscles}}{\text{mass of spider}}$.

Temperature is likely to be one of the most important factors influencing the work done by a given amount of muscle. Buchthal, Weis-Foch & Rosenfalck (1957) found that the twitch work of locust flight muscle increased by a factor of $\frac{5}{3}$ for an increase in 12° C. (20 – 32°). Thus temperature could account for jumps of 20 cm. performed by a South American salticid at an air temperature of 30° (we are grateful to Dr H. W. Lissmann for these observations). It might also account for jumps of 25 cm. reported by Pickard-Cambridge (1879) for *Attulus* ('*Attus*') *saltator* which lives on sandhills and in similar unsheltered environments which may get very hot on a sunny day.

The performance of salticid spiders in general compares very unfavourably with that of such jumping insects as the Acrididae. The jump of the latter is directly due

to the contraction of muscles which, owing to the gearing provided by the anatomy of the leg, may work at close to their optimal mechanical efficiency. In a hydraulic system the work which the muscles can do in a single contraction depends on the compliance (relation between dimensional changes and pressure) of the animal's body and on the volume change occurring at the leg joints. It appears that muscles operating such a system do so at considerably less than their optimum efficiency. However salticid spiders are small, so that although their absolute range is poor the range measured in terms of the body length is considerable, and this often has the greater biological significance.

SUMMARY

1. Photographs of the jumping spider *Sitticus pubescens* (Salticidae) show that the jump is almost entirely due to the sudden straightening of the fourth pair of legs. Multiple-image photographs show the importance of a silk drag-line in controlling the jump.

2. The torques at the leg joints have been estimated. Extension torques occur at the two hinge joints although these lack extensor muscles.

3. The erection of leg spines at the moment of the jump provides direct evidence that hydraulic forces are involved in the jump. This view is supported by estimates of the pressures involved, which fall within a factor of about two of those previously measured in the legs of the spider *Tegenaria*.

We are greatly indebted to Dr K. E. Machin for his advice on the analysis of the forces involved in the jump, and for reading the manuscript.

REFERENCES

- BROWN, R. H. J. & POPPLE, J. A. (1955). Multiple flash photography. *Med. Biol. Illustr.* **5**, 23-8.
 BUCHTHAL, F., WEIS-FOCH, T. & ROSENFALCK, P. (1957). Twitch contractions of isolated flight muscles of locusts. *Acta physiol. scand.* **39**, 246-76.
 PARRY, D. A. & BROWN, R. H. J. (1959). The hydraulic mechanism of the spider leg. *J. Exp. Biol.* **36**, 423-33.
 PICKARD-CAMBRIDGE, O. (1879). *The Spiders of Dorset*. Sherborne.

APPENDIX

This appendix shows in detail the method of calculating the torques at the joints of the salticid during a jump.

(a) *Calculation of the force acting at the foot* (see Text-fig. 3)

Let:

Take-off velocity = v cm./sec. (measured on film).

Take-off distance = s cm. (measured on film).

Mean acceleration = $\frac{1}{2}(v^2/s)$.

Mass of spider = m g.

Mean resultant force through centre of gravity (= mass \times acceleration) =

$$\frac{v^2 m}{2s} = F.$$

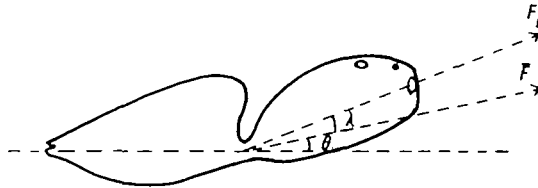
From a resolution of forces:

$$\text{Ground reaction } (F_g) = \frac{mg \cos \theta}{\sin \lambda}. \quad (\text{Ia})$$

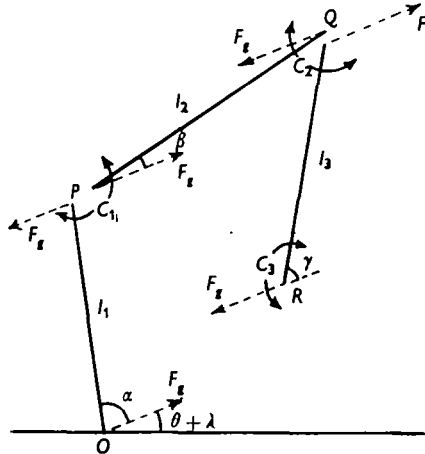
$$\tan \lambda = \frac{mg \cos \theta}{F - mg \sin \theta}. \quad (\text{Ib})$$

(b) Calculation of torques at the joints

In Text-fig. 4 let α , β and γ define the configuration of the leg, and l_1 , l_2 and l_3 be the lengths of the segments OP , PQ and QR respectively. Also let C_1 , C_2 and C_3 be the magnitudes of the equal and opposite torques at the joints P , Q and R .



Text-fig. 3



Text-fig. 4

Since the mass of a leg segment is small compared with that of the spider, it can be shown that changes of momentum and angular momentum can be neglected. Hence the sum of all the forces acting on a segment must be zero—i.e. the ground reaction F_g acting at the foot O will produce equal and opposite forces F_g at P , Q and R as shown (Text-fig. 4). Furthermore the sum of all the couples acting on a segment must also be zero. Thus:

(i) Segment OP (actually the two tarsal segments taken together) is acted upon by the anti-clockwise couple $F_g l_1 \sin \alpha$ and the couple C_1 . Calling clockwise couples positive:

$$-F_g l_1 \sin \alpha + C_1 = 0.$$

$$\therefore C_1 = F_g l_1 \sin \alpha.$$

(I)

(ii) Similarly segment PQ (actually tibia and patella taken together) is acted upon by the anti-clockwise couple $F_\theta l_2 \sin \beta$ and the couples $-C_1$ and C_2 , and

$$-F_\theta l_2 \sin \beta - C_1 + C_2 = 0.$$

Using (1): $C_2 = F_\theta (l_1 \sin \alpha + l_2 \sin \beta).$ (2)

(iii) Similarly segment QR (the femur) is acted upon by the clockwise couple $F_\theta l_3 \sin \gamma$ and the couples $-C_2$ and C_3 ; and

$$F_\theta l_3 \sin \gamma - C_2 + C_3 = 0.$$

Using (2): $C_3 = F_\theta (l_1 \sin \alpha + l_2 \sin \beta - l_3 \sin \gamma).$ (3)

(c) *A worked example*

The following calculation applies to the jump illustrated in Pl. 13:

Take-off velocity (v) = 67 cm./sec.

Take-off distance (s) = 0.44 cm.

Mean acceleration = 5,130 cm./sec.².

Mass of spider = 0.01 g.

Resultant force through centre of gravity (F) = 51.3 dynes.

Angle of take-off (θ) = 12°.

Ground reaction (F_θ) = 55 dynes (27.5 dynes per leg).

$\lambda = 10^\circ.$

Dimensions of leg segments: $l_1 = 0.18$ cm.; $l_2 = 0.22$ cm.; $l_3 = 0.19$ cm. Considering the disposition of the leg at the moment of take-off (Pl. 13, 2nd frame): $\alpha = 76^\circ$; $\beta = 12^\circ$; $\gamma = 58^\circ$.

Hence from equations (1), (2) and (3):

$C_1 = 4.8$ dyne-cm.; $C_2 = 6.1$ dyne-cm.; $C_3 = 1.6$ dyne-cm.

Similarly for the disposition of the leg shown in Pl. 13, 3rd frame:

$\alpha = 66^\circ$; $\beta = 12^\circ$; $\gamma = 84^\circ$.

$\therefore C_1 = 4.5$ dyne-cm.; $C_2 = 5.8$ dyne-cm.; $C_3 = 0.6$ dyne-cm.

Finally for the disposition of the leg shown in Pl. 13, 4th frame:

$\alpha = 21^\circ$; $\beta = 7^\circ$; $\gamma = 20^\circ$.

$\therefore C_1 = 1.8$ dyne-cm.; $C_2 = 1.1$ dyne-cm.; $C_3 = -0.7$ dyne-cm.

Note. The signs of C_1 , C_2 and C_3 in this worked example indicate the sense of the couples acting at each joint on the *distal* segment.

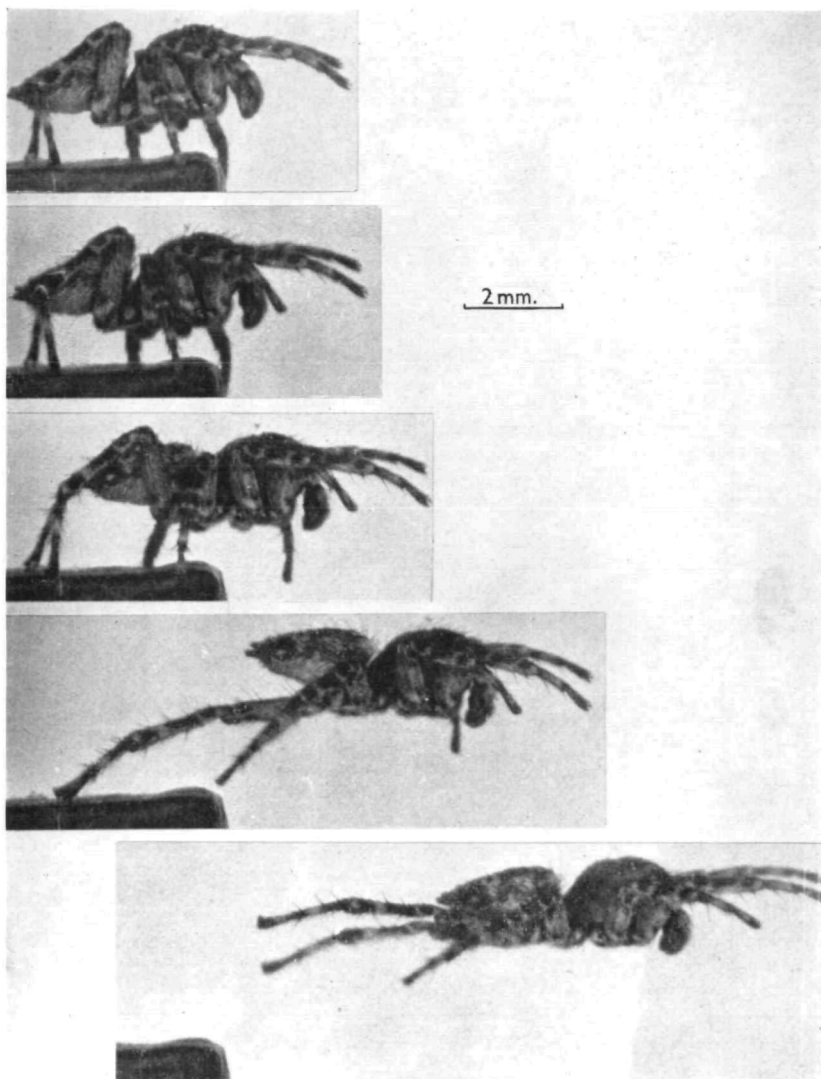
EXPLANATION OF PLATES

PLATE 13

Sitticus pubescens jumping. Frame interval 6 msec. Note the inflation of the articular membrane of the femur-patella joint, and the erection of the leg spines.

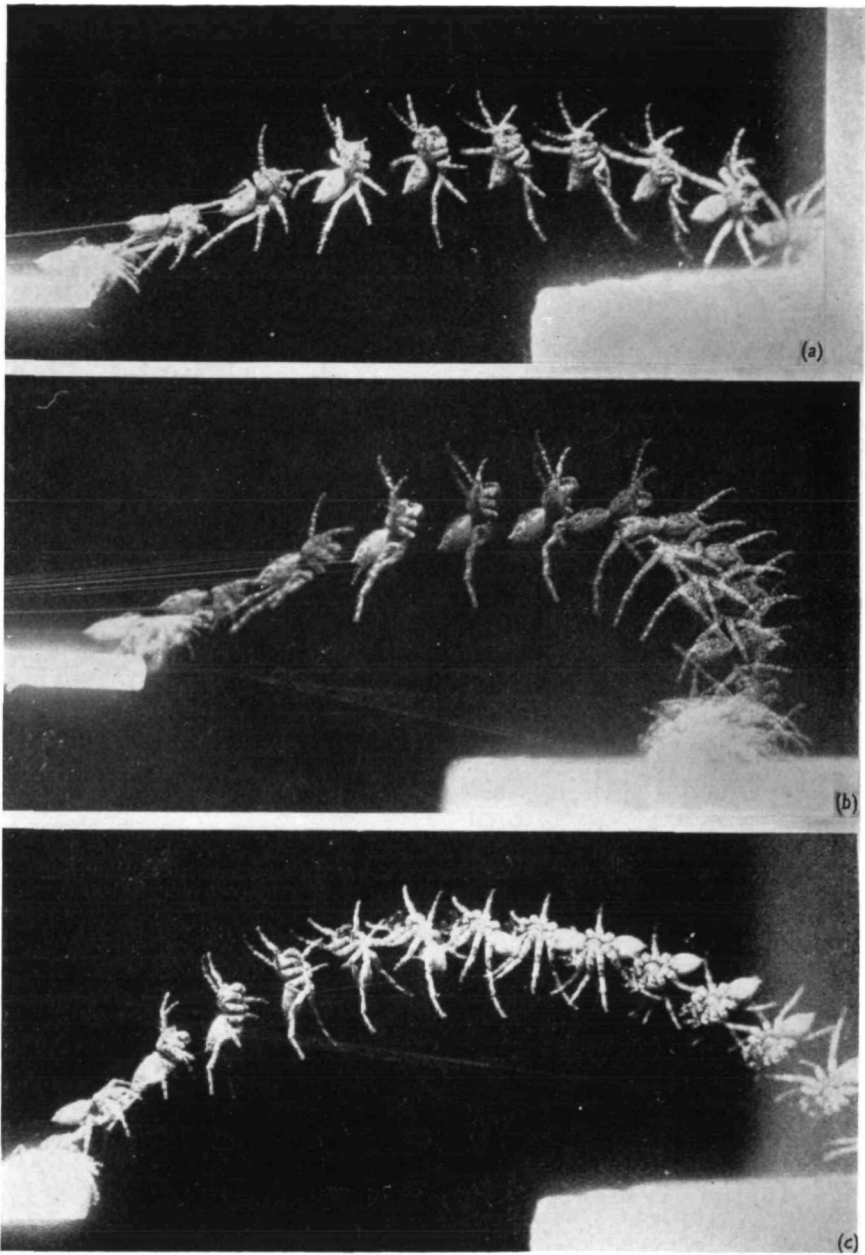
PLATE 14

Sitticus pubescens jumping, taken by multiple-flash photography (flash interval $7\frac{1}{4}$ msec.). In *a* the silk drag-line appears to be used to check counter-clockwise pitch; in *b* it is used to control range; while in *c* it appears to have broken and the spider makes a somersault.



PARRY AND BROWN—THE JUMPING MECHANISM OF SALTICID SPIDERS

(Facing p. 664)



PARRY AND BROWN—THE JUMPING MECHANISM OF SALTICID SPIDERS