

THE HYDRAULIC MECHANISM OF THE PREDATORY STRIKE IN DRAGONFLY LARVAE

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SUMMARY

1. *Aeschna* larvae catch prey with a fast-moving elongated labium. The mechanism of this movement was analysed by high-speed cinematographs and by hydrostatic and electrophysiological measurements.

2. The strike movement consists of an initial, mid and late phase. The angular acceleration of the joints of the labium is 2.6×10^5 and 7.8×10^5 deg. s⁻² during the initial and mid phase respectively. The torque necessary for the acceleration was calculated to be 1.3×10^{-5} and 4.0×10^{-5} N.m for the initial and mid-phases respectively.

3. The relation between the pressure applied to the labium and the extension torque at the joints has been established. No torque develops about the postmentum-prementum joint as long as the click of the flexed labium is engaged.

4. The power production of the extensor muscles is less than the power output of the mid phase. The power for the mid phase is derived from the internal body pressure developed by the contraction of the abdominal dorso-ventral muscles. The required pressure for the mid phase is about 60 cmH₂O if the resistance is neglected and 80 cmH₂O when the resistance is considered.

5. Abdominal dorso-ventral muscles contract 110-500 ms before the onset of the strike and the body pressure of the animal increases to a peak of 40-120 cmH₂O at the onset of the strike.

6. The geometry of the labial joints gives the primary flexor muscles of the labium a large mechanical advantage over the extensor muscles in the fully flexed labium, and allows the extensor muscles to contract almost isometrically.

7. The extensor muscles and the primary flexor muscles co-contract for 75-100 ms before the strike. The strike movement begins when the flexor muscles relax. The stored energy in the extensor system is released suddenly and disengages the click producing the initial phase. Once the click is disengaged the internal pressure produces the large torque to move the labium with great acceleration during the mid phase.

INTRODUCTION

Dragonfly larvae are aggressive predators, which catch their prey by protruding their labia with great rapidity. In *Aeschna eremita* full extension of the labium takes only 16-25 ms (Pritchard, 1965). The mechanism of the movement and the mus-

culature of the labium have been studied (Amans, 1881; Whedon, 1927; Munscheid, 1933; Snodgrass, 1954), but the function of the individual muscles in the movement of the labium has not been explained conclusively. Since there is no labial muscle that is large and powerful enough to produce the rapid movement, a hydraulic system was postulated to be the direct source of the power required for this movement because of the following indirect evidence: a quick contraction goes through the body when the labium is suddenly protruded (Munscheid, 1933); the anal valve is found to be closed at the moment when the bulge appears in the labial joint (Pritchard, 1965); in an anaesthetized specimen, compression of the abdomen and thorax results in a lifelike forward swing of the labium (Snodgrass, 1954); the rapid increase in blood pressure, which occurs when the anterior dorso-ventral muscles of the abdomen contract, is invariably followed by labial extension (Olesen, 1972).

The object of this paper is twofold: (1) to determine if the hydraulic pressure generated by the contraction of the abdominal muscles is sufficient to ensure the rapid movement of the labium (to answer this, the dynamics of the labial movement was analysed by means of high-speed stroboscopic photography and correlated with anatomical and hydrostatic studies); (2) to determine the mechanism which controls the rapid movement of the labium (in this regard, the sequence of the labial muscle activities during a strike was analysed electromyographically and correlated with the concomitant pressure change in the branchial chamber).

MATERIALS AND METHODS

Late instar larvae of *Aeschna nigroflava* Martin and *A. juncea* L. were used for this investigation. There was no discernible difference found in the strike mechanism between these two species. Unless otherwise stated, the text and illustrations refer to the larva of *A. nigroflava*. The experiments were performed mainly at a water temperature of 15–20 °C.

Cinematographic recording

The strike of the larva was induced by jerky movement of a spherical silicone resin dummy. The strike thus elicited was photographed either with an 8 mm movie camera at a speed of 24 frames.s⁻¹ from above or with a stroboscopic sequential camera from the side. The latter equipment consisted of a continuously running film-camera and a xenon discharge tube driven by a strobo-flash circuit. The animal was placed between the xenon discharge tube and the camera so that the strike sequence at a maximum speed of 200 frames.s⁻¹ could be obtained by this means. The relevant films were printed for further analysis.

Dead model experiment

The apparatus for measuring the internal pressure and the torque produced by the labium in the dead model is shown in Fig. 1. The head of an animal was isolated and fixed on to the end of the barrel of a 1 ml syringe with beewax-resin mixture. In some instances only the isolated labium was fixed on to the syringe barrel. The syringe was filled with 1.3% magnesium chloride solution to relax the muscle (Parry & Brown

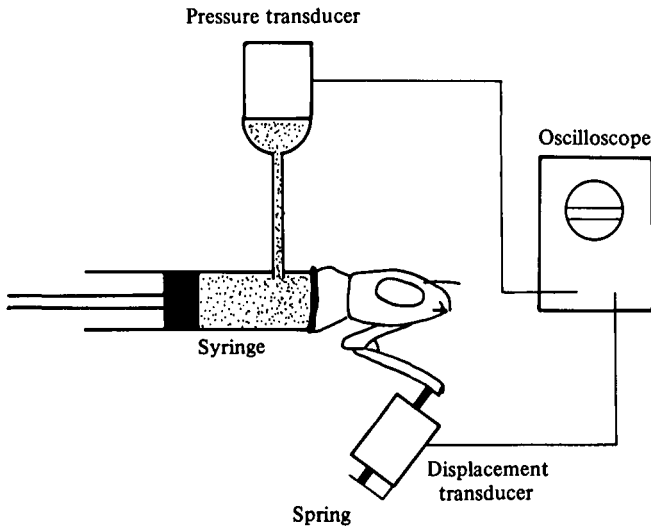


Fig. 1. Diagram of the method used for measuring the torque generated by the internal pressure applied to the labium.

1959). To record the internal pressure, polyethylene tubing was glued into the other end of the syringe through a small hole with cyano-acrylate and led to a pressure transducer (Toyo-Baldwin, MPU-0.5-290-0-III). Force was measured by a displacement transducer (San-ei Instr. Type 45071) equipped with return spring. Measured pressure was calibrated in cmH_2O ($1 \text{ cmH}_2\text{O} = 98 \text{ N.m}^{-2}$) with respect to a zero pressure, corresponding to a pressure which produced no torque around the labial joint. Outputs of these two transducers were displayed simultaneously on an oscilloscope.

In simulation experiments, extension of the labium in water was achieved with the same arrangement as above except the displacement transducer was eliminated so that the free movement of the labium, produced by increasing pressure, could be filmed at 200 frames $\cdot \text{s}^{-1}$.

Live tethered-animal experiment

The branchial chamber pressure and electrical activity of the respiratory dorso-ventral muscles were measured simultaneously in an animal glued to a polyethylene stick by its wing buds. The experimental chamber ($8 \times 12 \times 3 \text{ cm}$) was electrically grounded with stripped silver wire. Electromyograms were picked up by implanting $50 \mu\text{m}$ copper wire insulated but for the tip into the dorsal attachment of the respiratory dorso-ventral muscle of the 4th abdominal segment. Potentials were recorded between the recording electrode in the muscle and a grounded reference electrode. A short (12 mm) thin polyethylene tubing (1.6 mm in diameter) was inserted 10 mm into the branchial chamber through the anal valve of the animal and connected to a thicker tube (5.4 mm in diameter) that was then led to the pressure transducer. It was confirmed that this connexion produced no appreciable lag in pressure recording $\frac{1}{2}$ me. Zero pressure in this case was the hydrostatic pressure at which the animal was

placed. Labial movement was recorded by means of phototransistor and a beam of light which was interrupted by the extension of the labium. Recording of the electromyograms, pressure change and labial movement was simultaneously displayed on an oscilloscope and directly filmed.

Free-animal experiment

The animal moved freely in a cylindrical chamber (8 cm in diameter, 4 cm height) and the electrical activity of the labial muscles was recorded. The method to record the labial movement was the same as described above, but it was necessary to attract the animal near the phototransistor before each strike. In the freely moving animal, the reference electrode was implanted into the body cavity near the recording muscle electrode. Although strikes immediately after implantation of the electrodes appeared incomplete, a strike of full extent was achieved about 30 min later. The electromyogram together with labial movement was displayed on an oscilloscope and stored in a data recorder for later photography and analysis.

RESULTS

Anatomy of the labium

Both the structure and the musculature of the labium have been described by Snodgrass (1954), but there are some aspects to be added. The labium is divided into two parts, prementum and postmentum by an elbow-like joint (P-P joint) (Fig. 2). In a normal-size animal of 36 mm long, the prementum was 9 mm long and 4 mm wide and the postmentum 7 mm long and 2 mm wide. On either side of the distal end of the prementum, there is a pair of labial palps bearing a movable hook, the grasping organ of the animal. On the inner surface of the P-P joint, there is a strongly plicated fold of the articular membrane that extends laterally from a 'tubular membranous tongue' (Snodgrass) and bulges out during the strike. Also there exist a pair of click mechanisms near the P-P joint. A groove on the ventro-lateral side of the base of the prementum engages with a knob of the chitin in the ventro-lateral side of the elbow-like region of the postmentum. When the labium is in the folded position, they are engaged together. As the P-P joint begins to open, the knobs of the postmentum slide along the grooves of the prementum as if the engaged position is the real pivot of the P-P joint. Then the knobs suddenly disengage from the grooves. The result is that the pivot of the rotation moves from the engaged position to the hinge of the P-P joint and the volume of the articular membrane suddenly increases.

The postmentum is connected by the membrane to the ventral side of the head (P-H joint) and is supported by the T-shaped chitinous rod (hypopharyngeal apodeme of Snodgrass) which supports the posterior base of the postmentum and runs forward and downward to the base of the hypopharynx. During a strike, the posterior membrane of the P-H joint also expands but to a lesser extent than that of the P-P joint. Normally the labium is kept folded into the ridge of the ventral side of the head and the two expandable membranes are neatly folded with pleats between the joints.

The prementum contains four pairs of muscles: primary flexor muscles (*fxp*), secondary flexor muscles (*fxs*), tertiary flexor muscles (*fxt*) and extensor muscle

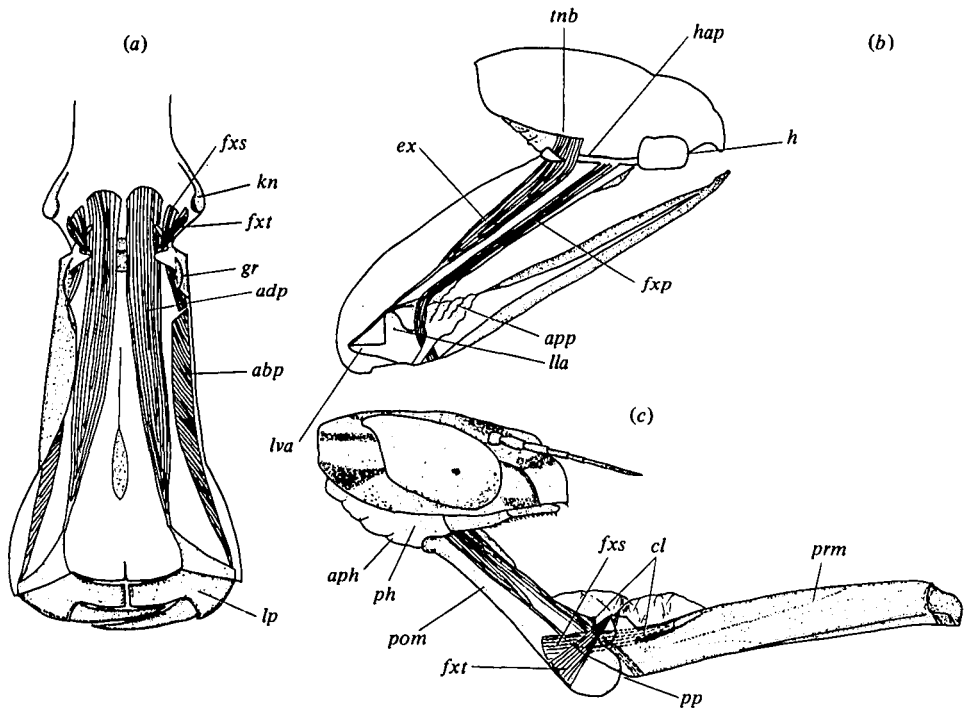


Fig. 2. The anatomy of the labium. (a) Dorsal view of the prementum. (b) Longitudinal section of the labium. Muscles of the elbow and prementum are removed. (c) Lateral view of the labium. *abp*, Abductor of labial palp; *adp*, adductor of labial palp; *aph*, articular membrane of the postmentum-head joint; *app*, articular membrane of the prementum-postmentum joint; *cl*, click mechanism of the labium; *ex*, extensor muscle; *fxp*, primary flexor muscle; *fxs*, secondary flexor muscle; *fxt*, tertiary flexor muscle; *gr*, groove of the click; *h*, hypopharynx; *hap*, hypopharyngeal apodeme; *kn*, knob of the click; *lp*, labial palp; *lla*, lobe of lever arm of prementum; *lva*, lever arm of prementum; *ph*, postmentum-head joint; *pp*, prementum-postmentum joint; *pom*, postmentum; *prm*, prementum; *tnb*, tentorial bar.

(*ex*) (Fig. 2). The primary flexor muscles attach side by side to the hypopharyngeal apodeme on the median ventral region of the base of the postmentum. When the labium is in the fully flexed position, the fold of the articular membrane pulls the flexor muscles inside the joint. Therefore, the muscles insert upon the ventral surface of the prementum anterior to the hinge nearly at right angles. The extensor muscles attach to the tentorial bar. They are heavy at the base but each tapers down to attach to a small cord-like tendon that pulls the 'lever arm' (Snodgrass) projecting from the prementum into the rounded elbow-like portion of the postmentum. They are also curved by the hypopharyngeal apodeme in the fully flexed position. The secondary flexor muscles, which are somewhat fan-shaped, have their origins on the lateral wall of the elbow-like region. From here they run a short distance to the ventro-lateral floor of the prementum. The tertiary flexor muscles are also fan-shaped muscles attached to the end of the postmentum laterad of the lever arm. They insert into the chitinous processes, i.e. the lobes of the lever arm from which the articular membrane extends around to the anterior side of the joint.

Two pairs of muscles are present in the prementum, abductors (*abp*) and adductors

(*adp*) of labial palps. The abductors lie wholly within the prementum. They are large flat muscles that are attached near the hinge and run to the outer side of the lateral lobes. The adductors are the largest muscles of the labium. They attach to the elbow-like region of the postmentum and insert into the tendons which are attached to the medial side of the labial palps.

Labial movement in the strike

There are two types of strikes, defensive and predatory, which differ from each other with respect to the direction and speed of the labial movement. Defensive strikes during which the labium is protruded upward, could be elicited by grasping the animal's thorax and vigorously brushing the dorsum of the head. In this study, we have analysed in detail more rapid movement of the labium during predatory strikes.

The initial event of all strikes was the opening of the labial palps, which began before the labium extended forward and which took 40–200 ms, with an average of 60 ms, at the normal water temperature, to open fully. The labium projected forward as soon as the palps were fully open. Occasionally the labial palps were opened a little but the labium was not extended. This occurred when the dummy prey was removed abruptly from the target range of the animal. Labial extension was complete usually within a single frame of motion picture at a speed of 24 frames. \cdot s⁻¹ and in no instance did completion take longer than 40 ms. Water temperature, which was probably also the muscle temperature, had no effect on the extension completion time even at temperatures as low as 5 °C. Thus the muscle contraction did not appear to be directly responsible for labial extension since the contraction time of muscle in general becomes longer as the temperature is lowered (Carvallo & Weiss, 1900). On the contrary, labial retraction time was affected by temperature, since it took an average of 430 ms to retract the labium at 5 °C and 100 ms at 20 °C.

With stroboscopic serial photographs at 200 frames. \cdot s⁻¹, we determined the position of the labium in 5 ms steps (Fig. 3). The angular changes of the two joints, P–P joint and P–H joint, during the strike were plotted as in Fig. 4. The angular velocities of both joints were calculated from these plots and graphed as in Fig. 5. The plots of the angular changes and angular velocities for both joints were similar. From the time course of the joint angle it was apparent that extension of the labium was complete by 25 ms after the start of the strike and the major part (80–90%) of the angular change occurred during the last 15 ms of the strike (Fig. 4).

Based on the time course of the angular velocity of both the P–P and P–H joints (Fig. 5) there appeared to be three phases during labial extension. There was an initial phase from 0–10 ms after the start of the strike, during which the angular velocity increased slowly and at the end of which the angles of the P–P and P–H joints were 30° and 50° respectively. The 30° angle of the P–P joint is slightly greater than the angle at which the labial clicks disengage. There was a mid phase from 10 to 20 ms after the start of the strike, during which the angular velocity increased rapidly to reach a maximum of 10×10^3 deg. \cdot s⁻¹ and 7.6×10^3 deg. \cdot s⁻¹ for the P–P and P–H joints respectively. When the angular velocity was maximum, the tip of the prementum moved at a linear velocity of 1.0 m. \cdot s⁻¹. It was at this moment that the prey was generally struck. An end phase occurred from 20 to 25 ms after the start of the strike

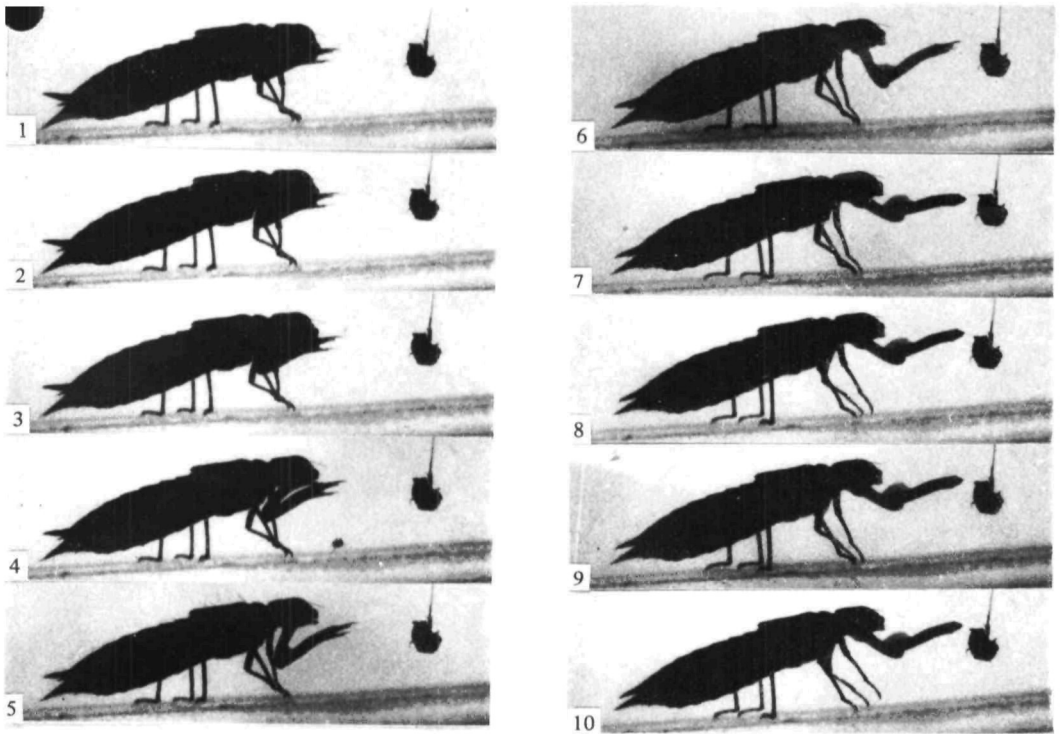


Fig. 3. A labial strike of intact *Aeschna nigroflava* larva taken by stroboscopic photography at the speed of 200 f.p.s. (interval between frames 5 ms). Frame no. 3 shows the beginning of the extension and frame no. 7 shows the full extension of the labium.

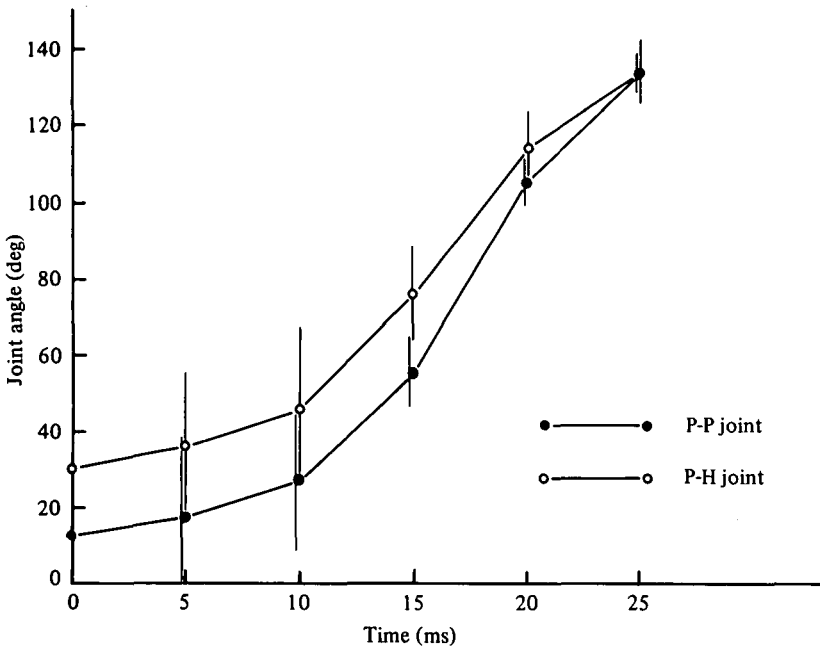


Fig. 4. Average angular changes of the prementum–postmentum joint (P–P joint, filled circles) and the postmentum–head joint (P–H joint, open circles) during strike movements with no actual prey catching. The number of trials is 15. Vertical lines are $\pm 1 \times \text{S.E.M.}$

during which the angular velocity fell rapidly, at which time the labium was fully extended and the labial palps were closed.

There was no lateral movement of the labium during the extension but the animal could vary the direction of the labial movement in the vertical plane by controlling the relation between the angle of the P–H joint and the P–P joint. For example, when the dummy prey was located near the bottom of the chamber, the animal slightly lowered its head and the angle of the P–P joint became greater than that of the P–H joint, enabling the labial palps to strike the prey.

Severance of the labial muscles, primary flexor muscles or extensor muscles caused an abnormal strike movement. When the primary flexor muscles were severed, the angle of the P–H joint remained immobile but the P–P joint opened rapidly, resulting in the labial palps hitting the bottom with such force that the animal was raised. Severing the extensor muscles caused the reverse effect, i.e. the angle of the P–P joint changed little and the angle of the P–H joint increased at a slower velocity than normal so that the palps snapped upward missing the target, which had been presented in front of the animal. This type of upward movement resembled that of a defensive strike.

Hydraulic system of the labium

The click mechanism, which exists at the P–P but not at the P–H joint, plays an important role in labial movement. No torque about the P–P joint was observed as long as the labium was fully flexed, the click was engaged and the internal pressure was

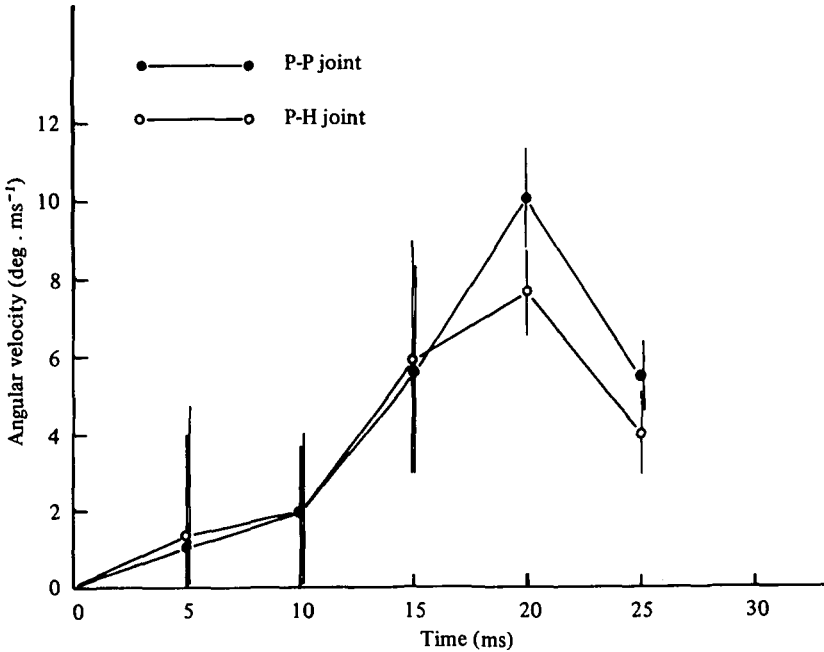


Fig. 5. Average angular velocities of the P-P joint (filled circles) and the P-H joint (open circles) calculated from Fig. 4. Vertical lines are $\pm 1 \times \text{S.E.M.}$

less than 120 cmH₂O. Since the clicks were not disengaged until the P-P joint angle was greater than 30°, the torque generated by the static pressure could only be measured when the P-P joint angle was greater than 30°, i.e. after the initial phase of labial movement. Once the P-P joint angle was greater than 30°, as the internal pressure was raised to 120 cmH₂O, the torque increased linearly to 1.5×10^{-4} N.m and 2.0×10^{-5} N.m around the P-P and P-H joint respectively (Fig. 6). On the other hand, once the P-P joint angle was greater than 30°, there was no discernible change in torque as long as the pressure was constant.

When the ventral nerve cord was severed between the suboesophageal and prothoracic ganglia, the animal could not contract its abdominal muscles in the predatory strike so that the hydraulic system was ineffective. The animal could survive for a few days after the operation and the animal's ability to strike returned about 1–2 h after the operation. However, the labium projected forward to only about one-third the length of the prementum and more slowly than in the intact animal. It would, therefore, appear that in the intact animal the muscles within the labium contribute the force necessary to extend the labium but the hydraulic system adds a force, which is necessary to extend the labium completely with maximum velocity.

Mechanics of the labial movement

A simplified model has been drawn from photographs of the dissected labium (Fig. 7). The labium is assumed to consist of slender rods with their pivots at each

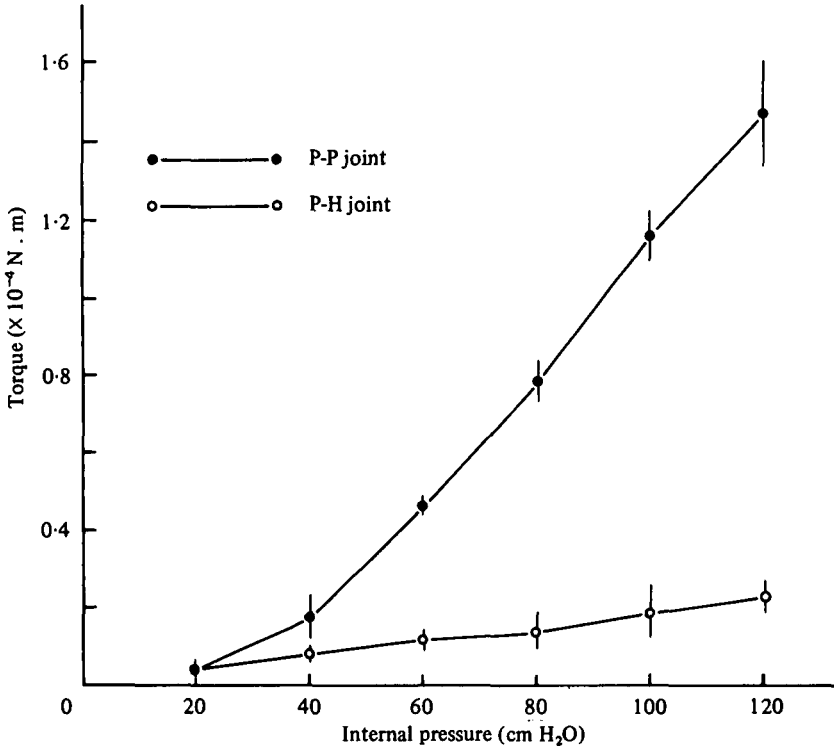


Fig. 6. Relation between the internal pressure applied to the labium and the torque generated about the P-P joint (filled circles) and the P-H joint (open circles) by the artificial pressure. Vertical lines are $\pm 1 \times$ s.e.m.

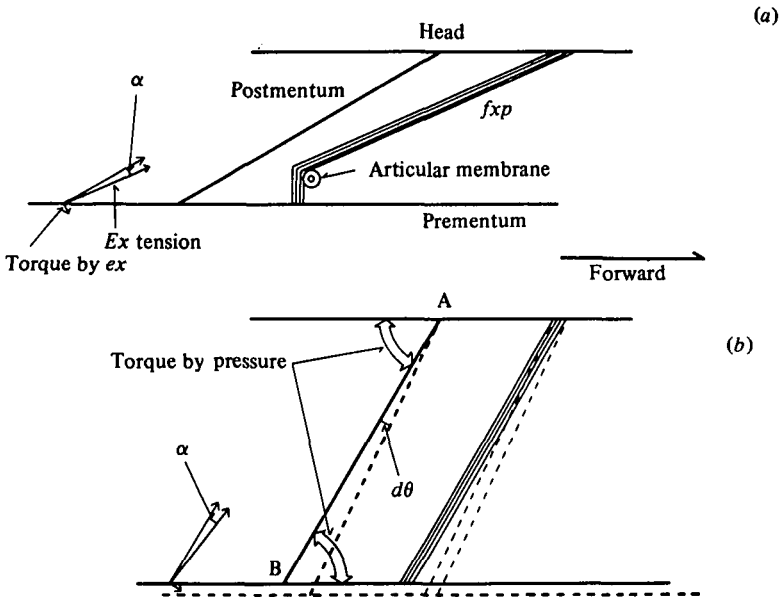


Fig. 7. Simplified schematic model of the labium. (a) The labium in the flexed position. (b) The labium partially extended. The thick lines represent a mechanical analogue of the labial structure. The dotted lines represent forward movement ($d\theta$) of the labium. α , The angle between the line of action of the extensor tendon and the line of postmentum.

end. Though the pivot of the P-H joint may change during a movement, the middle of the longitudinal axis of the T-shaped chitinous rod is assumed to be an effective pivot of the joint. This model has the following geometry. In the fully flexed labium, the angle between the line of action of the extensor tendon and the line of postmentum rod is 7° . This angle changes little during movement of the labium. As the fold of the articular membrane pulls the flexor muscle toward the inside of the P-P joint in the fully flexed labium, the flexor apparently exerts its tension on the prementum from the pivot where the flexor muscle is in contact with the fold of the membrane. The line of the postmentum rod makes an angle of approximately 70° to the line of action of the flexor tendon. Thus the flexor muscle has an 8:1 mechanical advantage over the extensor muscle in a fully flexed labium. The expansion of the articular membrane decreases this angle to approximately 0° .

In the situation where the flexor muscle has a constant length during a strike movement of the labium, the torque generated about the P-P joint is the same as the torque about the P-H joint (see Appendix). The kinetic energy of the prementum rod can be calculated with the condition that the same mass of the prementum rod is loaded at the distal end of the postmentum, because each portion of the prementum has the same velocity and direction at any moment during the motion. The torque to move the prementum rod can be calculated with this model and the speed of the movement of the model is controlled by the summed torque about the P-H joint.

To clarify the torque working on the labium during a strike, angular acceleration, A , is calculated by the formula:

$$A = \Delta v / \Delta t,$$

where Δv is the change of the angular velocity in Δt (5 ms). Since the angular velocity of both joints is similar, the angular acceleration was calculated from the data of the P-H joint. The change of the angular velocity in the P-H joint is $1.3 \times 10^3 \text{ deg. s}^{-1}$ each 5 ms during the initial phase and $3.9 \times 10^3 \text{ deg. s}^{-1}$ each 5 ms during the mid-phase. Thus the angular acceleration is $2.6 \times 10^5 \text{ deg. s}^{-2}$ during the initial phase and $7.8 \times 10^5 \text{ deg. s}^{-2}$ during the mid-phase. The angular acceleration in the mid-phase is roughly three times that in the initial phase. The total torque, T , about the P-H joint for the acceleration of the labium, neglecting internal friction and hydraulic resistance, is given by the equation:

$$T = (I_1 + I_2) \times A,$$

where A is the angular acceleration in radians. s^{-2} , I_1 is the moment of inertia of the postmentum about P-H joint and I_2 is that of the prementum about the P-H joint. I_1 and I_2 will be given by:

$$I_1 = M_1 \times L^2 / 3, \quad I_2 = M_2 \times L^2,$$

where M_1 and M_2 are the mass of the postmentum and prementum respectively and L is the length of the postmentum. M_1 , M_2 and L were 26 mg, 44 mg and 7.5 mm respectively. Thus the minimum torque was $1.3 \times 10^{-5} \text{ N.m}$ at the initial phase and $4.0 \times 10^{-5} \text{ N.m}$ in the mid phase. The pressure of 60 cmH_2O is sufficient to produce the required torque for the mid phase (Fig. 6).

Table 1. Comparison of the labial extensor muscle with locust tibia extensor muscle

Muscle ...	Labial extensor		Tibia extensor
	Initial	Mid	
Cross-sectional area (mm ²)	0.09		21
Weight (mg)	0.36		80
Tension (N.mm ⁻²)	0.08*	0.24*	0.75
Average power (W.g ⁻¹)	0.024*	0.60*	0.25

* Values calculated from actual strike movement. The data of the tibia extensor are from Bennet-Clark (1975).

The torque, T , that the extensor muscles produce about the P-H joint is given by the following equation:

$$T = L \times F \times \sin(\alpha),$$

where F is the tension of the extensor muscles, α is the angle between the line of action of the extensor tendon and the line of the postmentum and L is the length of the postmentum. The tension which the extensor muscles must produce is given by solving this equation for F , where T is 1.3×10^{-5} N.m and 4.0×10^{-5} N.m during the initial and mid-phase, α is 7° and L is 7.5 mm. Thus the tension is 1.5×10^{-2} N during the initial phase and 4.4×10^{-2} N during the mid phase.

The rotational kinetic energy, E_k , is given by

$$E_k = 1/2 \times I \times \omega^2,$$

where I is the moment of inertia and ω is the angular velocity in radians.s⁻¹. From Fig. 5, ω in the initial phase and in the mid phase was 34 and 170 radians.s⁻¹ respectively and I was 3.0×10^{-9} kg wt. m². Therefore, E_k is 1.7×10^{-6} J in the initial phase and 4.3×10^{-5} J in the mid phase. The cross-sectional area, weight, calculated tension and power of the labial extensor muscle were compared with the comparable system of the locust tibia extensor muscle (Table 1). The average power of the labial extensor was calculated assuming that the contraction time of the muscle was 100 ms. The calculated tension and power will be much higher when the hydrodynamic resistance and the internal friction is considered. Even in this situation, the tension of the labial extensor muscle may agree well with that of the locust tibia extensor muscle. However, the required power of the labial extensor muscle to produce the mid phase is considerably higher than that of the locust tibia extensor muscle. Thus the extensor muscle is unlikely to produce the mid phase of the strike if the muscle has a similar power production as the locust tibia flexor muscle.

Simulation of the strike

In order to study the internal mechanism, the strike was analysed under known artificial conditions. As described in the previous section, the internal pressure is a main source of the rapid labial strike. The strike movement in the dead animal was observed and filmed at 200 frames.s⁻¹ under known internal pressure. The labium was fully extended by artificial pressure and then retracted forcibly with forceps to the

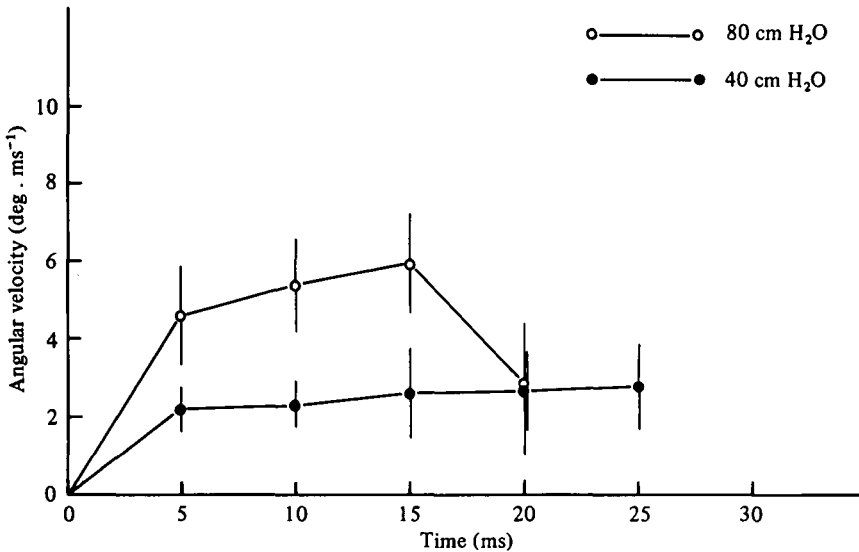


Fig. 8. Angular velocity of the labium about the P-P joint measured from simulated strikes under 80 cmH₂O (open circles) and 40 cmH₂O (filled circles) with disengaged click. Vertical lines are $\pm 1 \times \text{S.E.M.}$

position where the click had just disengaged. When the forceps were removed, the labium re-extended in a manner similar to a normal strike, the labial extension being complete within 25–30 ms. Application of a pressure of 80 cmH₂O accelerated the labium sufficiently to simulate the mid-phase of the normal strike (Fig. 8). The angular velocity increased for an initial 5 ms, remained almost constant for 10–15 ms, and then decreased to zero. The acceleration produced by the application of a pressure of 40 cmH₂O was only half of that with 80 cmH₂O and two times larger than the value of the initial phase of a normal strike. A pressure of 80 cmH₂O produced a torque of 9.1×10^{-5} N.m (Fig. 6): this is about two times greater than that determined disregarding resistance during the mid phase of a normal strike. The torque produced by the pressure of 40 cmH₂O was 2.7×10^{-5} N.m – a figure about two times greater than the calculated torque during the initial phase.

When the click remained engaged, an increase of pressure resulted in an abnormal labial movement. At first, the angle of the P-H joint started to open but the P-P joint remained folded. As the postmentum swung forward, the P-P joint was forced to open by collision with the mouth, which caused the click mechanism to disengage, resulting in rapid opening of the P-P joint. The extensor muscle of the labium seems to disengage the click in a normal strike.

Muscle activity and the change of the body pressure during a strike

During the pre-strike period, the respiratory dorso-ventral muscle, primary flexor muscle, extensor muscle and abductor muscle were active. The activity of the respiratory dorso-ventral muscle began first during the pre-strike period, 110–500 ms before the onset of the strike, and the frequency of the potentials increased gradually. The initial low frequency in the burst was associated with the gradual increase of pressure.

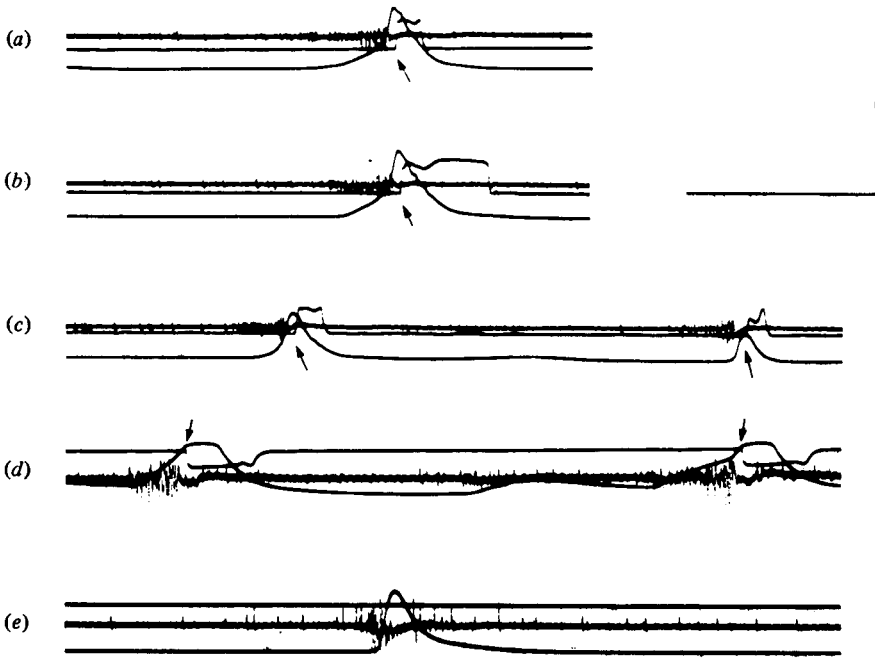


Fig. 9. (a-c) Electrical activity of the respiratory dorso-ventral muscle (top trace) and branchial chamber pressure (bottom trace) during strike movement (middle trace), where upward deflection indicates extension of the labium. (b) Successful strike. (a, c) Failed strike. Arrows in this and following figures indicate onset of strike. (d) Electrical activity of the respiratory dorso-ventral muscle (middle trace) and branchial chamber pressure (bottom trace) during strike movement (top trace) in water temperature of 5 °C. (e) Respiratory dorso-ventral muscle activity (middle trace) and branchial chamber pressure (bottom trace) during an episode of swimming. Ordinate, 100 cmH₂O; abscissa, 500 ms.

The measured branchial chamber pressure, assumed to be the body pressure working on the labium, began to rise 50–350 ms before the start of the strike and reached a peak of from 40 to 120 cmH₂O at the onset of the strike (Fig. 9a-d).

The primary flexor muscle activity began 100–150 ms prior to the strike (Fig. 10a, b), i.e. about the same time as the branchial chamber pressure began to increase. The frequency of a single unit gradually increased to a peak of 280–320 Hz, and this increase in frequency was associated with an increase in the action potential amplitude. Activity of the extensor muscle began later than that of the primary flexor muscle, i.e. 75–100 ms before the onset of the strike (Fig. 10c, d). Therefore the primary flexor and the extensor muscles co-contract for about 100 ms before the onset of the strike. The frequency of the extensor activity rose more rapidly than the primary flexor activity to a peak frequency of less than 280 Hz at the same time as the primary flexor activity attained peak frequency. The activity of the abductor began 125 ms before the onset of the strike and continued for 100 ms (Fig. 11a). A few spikes were seen after the burst. The frequency of the pulse gradually increased to 400 Hz.

The dorso-ventral muscle activity ceased 20 ms before the onset of the strike so that there was a delay between the end of the electrical activity and the development of the maximum pressure. The start of the strike movement was marked by the cessation of

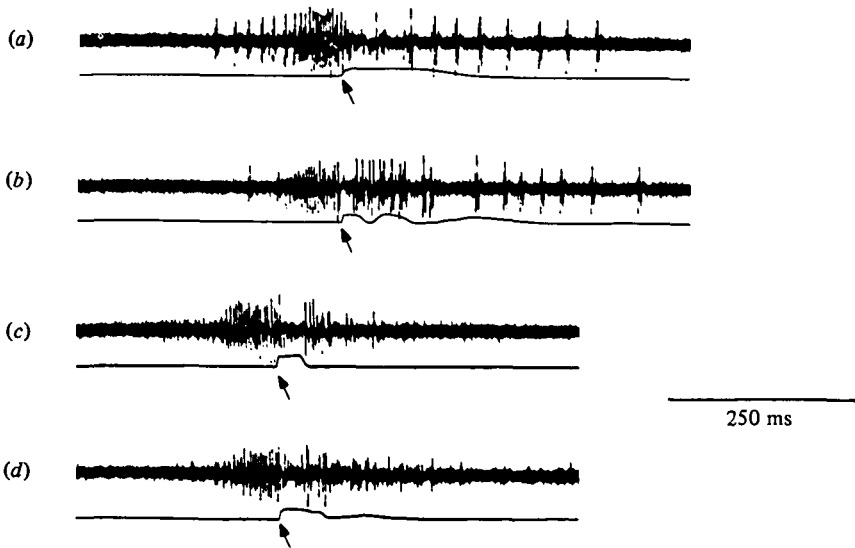


Fig. 10. (a, b) Electrical activity of the primary flexor muscle (*fxp*: upper trace) during strike movement of the labium (lower trace). (c, d) Electrical activity of the extensor muscle (*ex*: upper trace) during strike movement of the labium (lower trace). (b, d) Successful strike. (a, c) Failed strike.

the primary flexor muscle. Usually the activity ceased about 5 ms before the onset of the strike. In some cases the labial movement began as soon as the activity ceased, but there was a clear decrease of action potential frequency preceding complete cessation (Fig. 10*a*). The extensor activity was maintained for 80–120 ms so that it continued for 5–20 ms after the extension of the labium. The pressure decreased to zero in the following 100 ms, but at a low temperature of about 5 °C, the peak pressure was maintained for about 100 ms (Fig. 9*d*). The energy expenditure of a strike is much less than the total stored energy in the cuticle.

During swimming the duration of the burst of the dorso-ventral muscle potentials was short and the frequency of the muscle potentials was high from the start of the burst. The potentials ceased 30 ms before the pressure reached its peak value, 65 cmH₂O, which was similar to that recorded during the strike and which was achieved rapidly (Fig. 9*e*).

The adductor muscle was activated 20 ms before the onset of the strike, and the tertiary flexor muscle was spontaneously active at 10 Hz. The activity was also seen in the primary and secondary flexor muscles after the strike. The frequency of the electrical activity of these muscles was higher and the duration of these was longer in the successful strike than in the failed strike (Fig. 10*a, b, 11 b-f*). The sequence of the muscle activity described here is summarized in Fig. 12.

DISCUSSION

Storage of energy and its release

The movement of the labium in the predatory strike of the dragonfly larva is extraordinarily fast, because the muscular energy is stored during the preparatory period of the strike. Animals having a similar energy storage mechanism have one

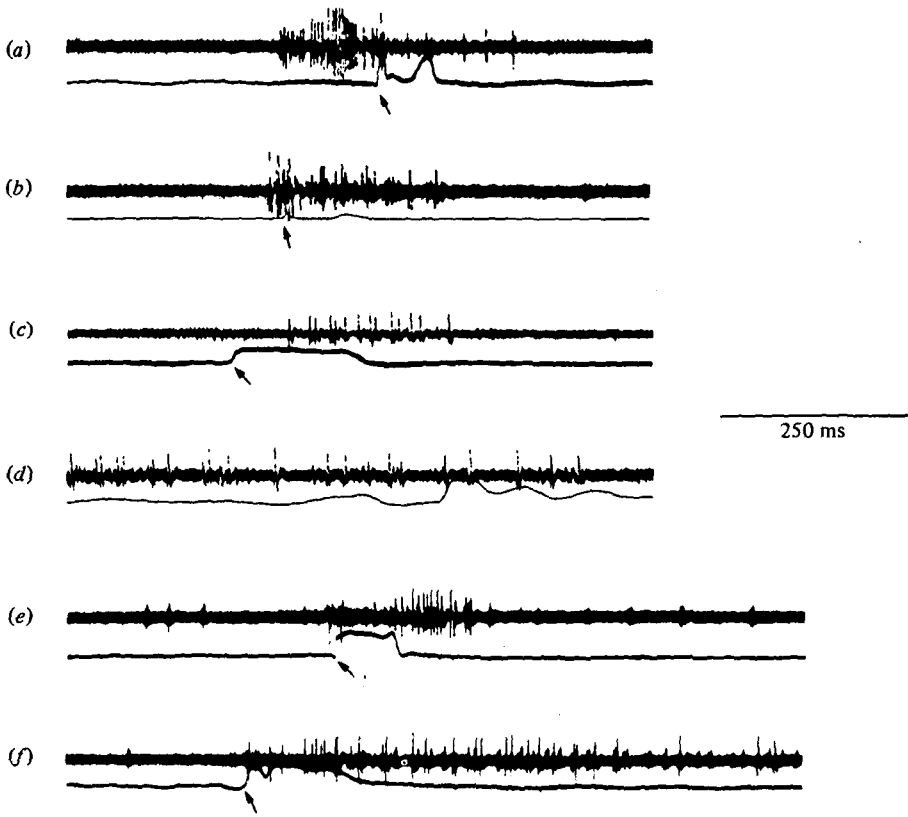


Fig. 11. Lower trace of each record indicates movement of the labium. (a) Electrical activity of the labial palp abductor (*abp*) during a strike. (b) Electrical activity of the labial palp adductor (*adb*) during a strike. (c, d) Electrical activity of the secondary flexor muscle (*fxs*) during a strike (c) and during a holding of a prey (d). (e, f) Electrical activity of the tertiary flexor muscle (*fxt*) during a failed (e) and successful strike (f).

common characteristic, i.e. the resultant movement is relatively insensitive to temperature change. This characteristic is quite advantageous for those behaviour patterns which require great velocity such as the escape jump or the predatory strike. In the jump of the locust (Brown, 1967; Godden, 1969, 1975; Heitler, 1974; Bennet-Clark, 1975; Heitler & Burrows, 1977) and in the predatory strike of the mantis shrimp (Burrows, 1969) the energy for the movement is generated by the extensor muscle, which contracts isometrically for a few hundred milliseconds, and is stored in the extensor system. In the jump of the flea, the required energy is stored as the compression of the resilin pad (Bennet-Clark & Lucey, 1967; Rothschild *et al.* 1972). The stored energy is released by disengaging the click in these animals.

There are two energy productive systems for the strike of the dragonfly larvae: a labial extensor-flexor system and an abdominal pressure raising system. The former system produces energy by almost isometric contraction of the extensor muscles. The produced energy must be stored largely in the mechanical elements, tentorial bar and lower arm of the prementum (Alexander & Bennet-Clark, 1977). The latter system

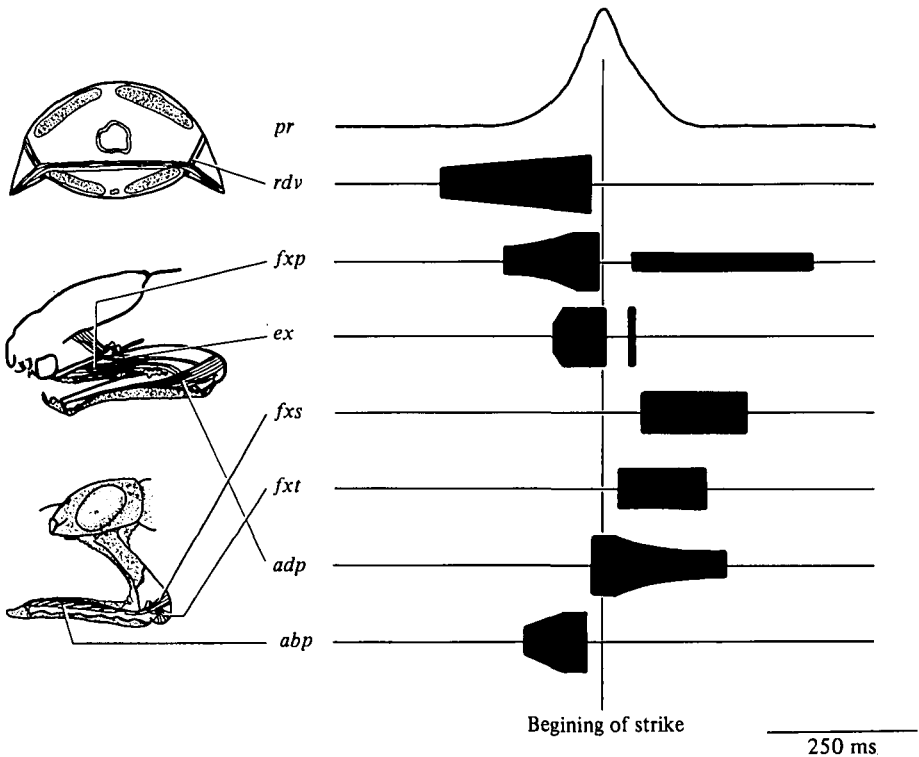


Fig. 12. Summarized schema of electrical activity of the various muscles and the branchial chamber pressure change during a strike movement of the labium. Thickness of the line of each muscle activity represents the frequency of the burst. Left top diagram shows the transverse section of the abdomen across the anterior margin of segment 6. *pr*, branchial chamber pressure; *rdv*, respiratory dorso-ventral muscle; other abbreviations are as in Fig. 2.

must involve other abdominal muscles as well as the respiratory dorso-ventral muscles, as used in the jet propulsion (Mill & Pickard, 1975), and the produced energy is stored as the strain-energy in the cuticle of the abdomen.

Since the primary flexor has a mechanical advantage over the extensor and the torque about the labial joints is small in the fully flexed labium, flexor activation keeps the labium in the flexed position during the energy storing process. Usually a strike movement occurs after the electrical activity of the primary flexor ceases. During the initial phase of the strike, the energy stored in the elastic component of the extensor system and the pressure at the P-H joint suddenly produce the torque, which protrudes the labium slowly. The power production of the extensor muscle cannot account for the power output of the mid phase of the labial movement. The energy produced and stored by the extensor muscles appears to be fully expended during the initial phase. The movement of the initial phase disengages the click mechanism of the labium suddenly, marking the beginning of the mid phase. A large torque about the P-P joint is then generated by the expansion of the articular membrane, causing the labium to move with full acceleration. The labial extensor-flexor system is not substantial for the rapid movement and the full relaxation of the flexor is not necessary

The mid phase where the hydraulic system is responsible for the movement. Instead, residual flexor tension may serve to stabilize the direction of the labial extension.

There is a latent period between the electrical activity and mechanical response in the muscle and it takes time to achieve peak tetanic tension. The electrical activity of the adductor of the labial palps begins 20 ms before the onset of the strike, so that this muscle has no effect upon the strike movement of the labium. This conclusion is supported by the fact that the palps are opening during strike movement.

Co-ordinated muscle activity

The activity sequence among the muscles and the change of the pressure which control the labial movement are practically stereotyped (Fig. 12), suggesting that there must be a central motor programme that co-ordinates the motor activities of various parts of the body. There are many interesting facets of this motor programme. One question is how far the programme can go before it is irrevocable, since a strike does not always occur when the labial palps are slightly open and when there has been activity of the dorso-ventral muscles, which usually precedes the activity of the labial palps abductor muscle. Under these circumstances the motor programme of the strike has already started but may be stopped. Thus a crucial time, after which the strike is irrevocable, may exist during the opening of the labial palps.

Another question is when the time of onset is determined. Although the onset of the strike occurs shortly after the cessation of the primary flexor activity, it is doubtful that cessation of the flexor activity alone determines the time of onset, since the strike always occurred when the change in pressure was maximal. There was no case in which the pressure was kept at a constant high value before the onset of the strike. It is likely that cessation of the activity of the dorso-ventral muscle is correlated with cessation of the primary flexor muscle activity. It would, therefore, appear that the beginning of the strike is marked by the time of the cessation of the activity of the dorso-ventral muscle or just prior to it. Peripheral feedback from pressure sensors does not seem to be responsible for the onset of the strike, because the peak pressure at the strike varies widely.

Advantage of the hydraulic system

There are two advantages for dragonfly larvae in using hydraulic pressure. First, a hydraulic system can be a multifunctional power source, and it may be economical for the neuromuscular system. In dragonfly larvae, hydraulic pressure is utilized in respiratory movement (Mill & Hughes, 1966; Hughes & Mill, 1966), in jet propulsive movement (Hughes, 1958; Hughes & Mill 1966; Mill & Pickard, 1975) and in the predatory labial extension. In *Aeschna*, the peak pressure of the branchial chamber was 2–5 cmH₂O for respiration and 25–40 cmH₂O for jet propulsion respectively (Hughes & Mill, 1966). The pressure in our experiment is measured under iso-volumetric condition, which is characteristic during labial extension because the anal valve is closed. Thus the pressure shows relatively higher values. The anal valve plays an important role in the motor programme of the labial strike and jet propulsion, though it is not clear whether the other part of the programme controlling the abdominal muscles is the same or not in both behavioural repertoires.

A second advantage of the hydraulic system is the separation of the power source and control mechanism. The raptorial leg of the mantis shrimp resembles the labium of the *Aeschna* larvae in its shape and high speed, but the leg is considerably large relative to the body size (Burrows, 1969). The dragonfly larvae can recruit the muscles distributed widely in the abdominal body wall instead of the restricted space of an appendage. Thus the dragonfly larvae have no need to have a large mass of muscles and appendages in order to produce the mechanical energy. In addition, small muscles in the labium control the hydraulic pressure, which produces high power output. This simplification of the internal structure of the head appendage may have many other advantages. However, these advantages demand more complex neural network, which must be responsible for the motor programme controlling the muscles of the abdomen as well as the head appendages.

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APPENDIX

In Fig. 7 (*b*) let us suppose that the model is under equilibrium by the retraction torque about the pivot A , T_a , and the extension torque about the pivot B , T_b . If this model is moved forward at the angle of $\delta\theta$ by the T_b , the work, W_a that T_a does is given by the following equation:

$$W_a = -T_a \times \delta\theta.$$

The work, W_b that T_b does is given by

$$W_b = T_b \times \delta\theta.$$

From the principal of virtual work,

$$W_a + W_b = -T_a \times \delta\theta + T_b \times \delta\theta = (-T_a + T_b) \times \delta\theta = 0.$$

This gives

$$T_a = T_b.$$

Therefore the torque produced about the pivot B can be converted to the torque produced about the pivot A .