THE OPERATION OF THE LABIUM IN LARVAL DRAGONFLIES

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The operation of the larval labium in dragonflies is reviewed and compared with other fast actions in other arthropods. The dragonfly labium is similar to most of these in that a locking mechanism allows energy storage prior to the action, but differs in that its successful operation requires coordinated and rapid operation of two joints, not just one. The locking mechanism resides in the primary flexor muscle of the labium, which alone appears to allow energy for the operation of both joints to be stored and prevents the labium from being protracted during jet propulsion.

INTRODUCTION

The structure and operation of the odonate larval labium (Fig. 1) are unique and much attention has been paid to them. Even so, the mechanics of the predatory strike have still not been described in a totally satisfactory manner. It is the purpose of this paper to review work on the operation of the labium and to compare the emerging picture with other fast actions in arthropods.

THE OPERATION OF THE LABIUM IN HISTORICAL PERSPECTIVE

SNODGRASS (1954) drew attention to the fact that, although the operation of the prementum-postmentum joint could be explained by labial muscle action, there are no muscles within the labium capable of operating the postmentum--head joint. He advanced an hydraulic explanation that was based on an old idea by AMANS (1881) for this part of labial protraction. Support for this hydraulic mechanism, with force generated by thoracic and abdominal muscles, subsequently came from observations that the anus closed just prior to labial extension and the membranous cuticle at the prementum-postmentum joint bulges when

the labium is extended (PRITCHARD, 1965), and that pressure changes in the thorax, correlated with electrical activity in muscles of the thorax and abdomen, occur during labial protraction (OLESEN, 1972).

However, this mechanism by no means fully explained labial action. In particular, the following observations were in need of clarification:

(1)   The pressure waves responsible for labial extension and jet propulsion are produced by contraction of the same set of muscles (OLESEN, 1972). During labial extension the anus closes and prevents jet propulsion. But what prevents labial extension during jet propulsion?

(2)   The postmentum moves slowly forwards before the actual strike, and then is released rapidly (CAILLIERE, 1972; cf. also Fig. 1).

(3)   The labium can be extended in dead larvae by squeezing on the body. However, the action is much slower than in the normal strike (PRITCHARD, 1976).

(4)   Extension of the labium is more than 3x faster than the strike of the praying mantis (ROEDER, 1959).

These points imply a locking mechanism in the labium during jet propulsion and during pressure build-up preliminary to labial extension. I postulated (PRITCHARD, 1976) that this locking mechanism resided in the flexor muscle of the prementum, a muscle that originates at the base of the T-shaped hypopharyngeal apodeme. My hypothesis was that the primary flexor muscle is actually contracted during the early stages of pressure build-up, thereby preventing labial protraction. I proposed the following sequence of events:

(1)   Palps open; flexors *and* extensors contract.

(2)   Anus closes; thoracic and abdominal muscles contract.

(3)   Flexors relax; apodeme bends as body cavity pressure surges forwards; extensors extend prementum; palps close.

(4)   Extensors relax; flexors contract again; thoracic and abdominal muscles relax; apodeme returns to resting position.

In 1979, OLESEN published further on the abdominal pump and proposed that the maxillae might be involved in the labial locking mechanism. In a post-script, he referred to my proposed locking mechanism, correctly pointed out that my model predicts electrical activity in the primary flexor muscles just before labial protraction, and stated that both his and my hypotheses are testable by electromyographic analysis.

Such a test was actually performed by TANAKA & HISADA (1980). This elegant study far surpasses the simple model I presented in 1976, but provides a convincing confirmation of the main points of my hypothesis, especially the order of contraction of the labial muscles. Tanaka & Hisada found that in *Aeshna* larvae the extensor muscles and the primary flexor muscles of the prementum co-contract for 75-100 msec before the flexors relax, at which time the strike begins. However, they also propose that the disengagement of a cuticular catch

mechanism and the internal pressure generated by the body wall musculature allows the rapid phase of labial extension, rather than the relaxation of the flexor muscles and the release of tension in the extensor muscles as I had proposed.

However, working with *Anax imperator*, PARRY (1983) has criticised some of the calculations of TANAKA & HISADA (1980) and concludes that the prementum-postmentum joint is unlikely to operate by blood pressure, and that no catch mechanism exists. If Parry is correct (and I have not been able to find a catch mechanism either) then release of the primary flexor tension probably is the mechanism that allows the rapid extension of the prementum by the premental extensor.

DISCUSSION

There is a wide range of fast actions in arthropods, but the mechanisms for almost all of them are very similar. The simplest is the predatory strike of praying mantids, in which the extensor muscles act directly without prior energy storage (GRAY & MILL, 1983). The others all involve energy storage before the release, either by means of a cuticular catch mechanism and/or by co-contraction of antagonistic muscles. Thus, in the jump of the flea, *Spilopsyllus cuniculi*, "the main impulse comes from the depression of the metathoracic femur, whose depressor muscle originates on the notum. In the resting position the attachment of the depressor tendon to the femur is over-centre with respect to the trochanter- -femoral joint. When the muscle contracts, energy is stored in a resilin pad located between notum and pleuron. This energy is released by a second muscle which pulls the depressor tendon away from the over-centre position, thus enabling it to depress the femur" (BENNET-CLARK & LUCEY, 1967).

The jump of the click beetle, *Athous haemorrhoidalis*, "involves a jack-knifing movement whereby a prosternal peg is slid very rapidly down a smooth track into a mesosternal pit. The muscles which produce this movement are allowed to build up tension by a friction hold on the dorsal side of the peg" (EVANS, 1972). Snapping shrimps of the family Alpheidae have at least 2 different types of catch mechanism (RITZMANN, 1974), but the rapid closure of the dactyl on the propus is brought about in the same manner, namely by contraction of the closer muscle until the force holding the two units apart is overcome.

The strike of mantid shrimps (Stomatopoda) and the jump of the locust *Schistocerca gregaria*, employ flexor muscles to counteract the action of the extensors, just as in the proposed mechanism for labial extension in dragonfly larvae. However, the extensor muscles in these first 2 arthropods are very much larger than the flexors and further specializations are necessary in order to prevent the joint opening under extensor tension. In mantid shrimps, "the flexor muscles begin to contract first, often 1 sec before the strike, so pulling a sclerite over a stop on the ventral wall of the merus. This gives them a 900:1 mechanical

advantage over the extensor muscles.... The flexor muscles relax just prior to the strike so that the sclerite then snaps over its stop on the merus allowing the stored energy of the extensor muscles to be delivered suddenly" (BURROWS, 1969). In the locust, "the geometry of the joint gives the flexor muscle a very large mechanical advantage over the extensor in the fully flexed position. This mechanical advantage decreases rapidly as the joint extends so that the residual flexor tension does not slow down movement. There is also a locking device associated with the flexor tendon which is engaged when the tibia is fully flexed" (HEIT-LER, 1974).

Of all of these mechanisms, the operation of the locust metathoracic leg is the closest to the action of the larval dragonfly labium about the premental-postmental joint. Although some sort of specialized catch mechanism in the latter has not yet been confirmed, its presence may not be necessary to allow for the storage of energy in the extensor muscle, since the extensor muscle is not much larger than the primary flexor and "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"(TANAKA & HISADA, 1980). This locking of the prementum on the postmentum will also prevent the labium from being rapidly protracted by blood pressure at the postmentum-head joint. Note in Figure 1 how the postmentum swings forward slowly in frames 1-9, but this is counteracted by contact between the prementum and the head (specifically, the labrum). The forward movement of the postmentum actually stops in frames 8 & 9. It is only when the primary flexors relax and the extensors can open the prementum-postmentum joint (Fig. 1, frame 10) that the prementum is no longer forced against the underside of the head and the postmentum-head joint can also open rapidly. Prior to this, energy has been stored in the muscles and cuticle of the body wall.

Thus the dragonfly larval labium appears to represent a relatively unspecialized form of energy storage mechanism. However, in other respects it is a more sophisticated device than any of the examples of fast actions in arthropods in that its successful operation demands coordinated and rapid operation of two joints, not just one. The locust jump, the flea jump, the mantis shrimp strike, the snapping of alphaeid shrimps, and the click beetle jump, depend on power being delivered rapidly to a single joint. If the larval dragonfly labium operated only through the prementum-postmentum joint it would not be protracted, but would simply slap down onto the substrate below the head.

The configuration of the dragonfly labium is basically identical to that of the praying mantid foreleg. The advantage of this configuration over that of the mantis shrimp is that it can achieve a greater reach. But the dragonfly larva and the mantis shrimp are able to store energy prior to the strike, which the praying mantid cannot. This means a faster strike and, more importantly, a power output that is not affected by temperature (BENNET-CLARK, 1975). A further advan-
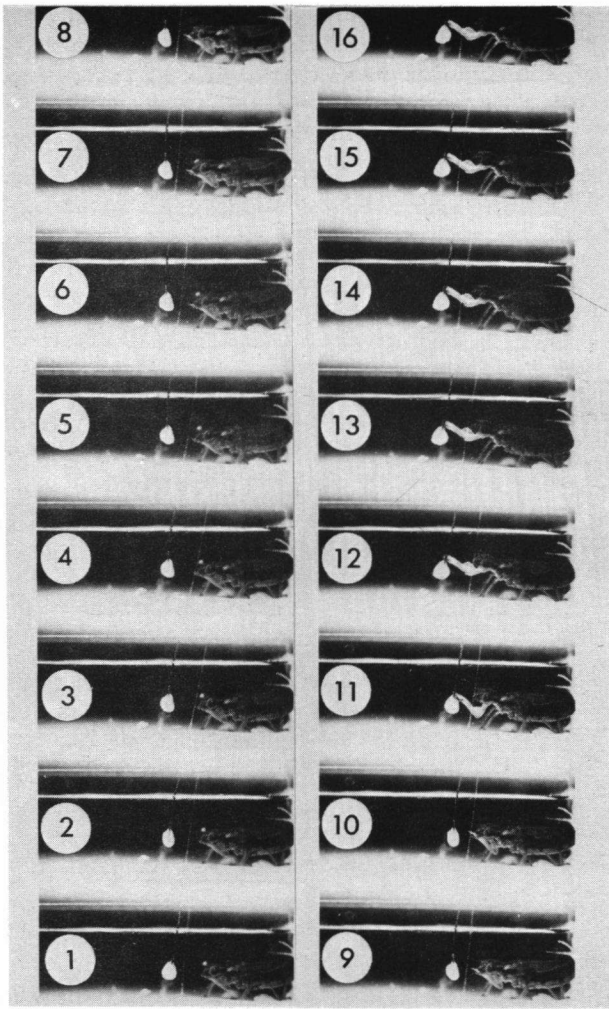
Fig. 1. Labial protraction in an *Aeshna canadensis* Walker larva. Interval between frames is 10 msec.

tage to the dragonfly larva alone is that the involvement of an hydraulic mecha-
nism allows the labium to be relatively small. And finally, the primary flexor
muscles of the labium alone provide the power which operates the locking
mechanisms and allows energy for the operation of both joints to be stored prior
to use, and prevents the labium from being protracted during jet propulsion.

REFERENCES

AMANS, P., 1881. Recherches anatomiques et physiologiques sur la larve de l'Aeshna grandis. *Revue Sci. nat., Montpellier* (III) 1: 63-74.

BENNET-CLARK, H.C., 1975. The energetics of the jump of the locust Schistocerca gregaria. *J. exp. Biol.* 63: 53-83.

BENNET-CLARK, H.C. & E.C.A. LUCEY, 1967. The jump of the flea: a study of the energetics and a model of the mechanism. *J. exp. Biol.* 47: 59-76.

BURROWS, M., 1969. The mechanics and neural control of the prey capture strike in the mantid shrimps Squilla and Hemisquilla. *Z. vergl. Physiol.* 62: 361-381.

CAILLIERE, L., 1972. Dynamics of the strike in Agrion (syn. Calopteryx) splendens Harris 1782 larvae (Odonata: Calopterygidae). *Odonatologica* 1: 11-19.

EVANS, M.E.G., 1972. The jump of the click beetle (Coleoptera, Elateridae) — a preliminary study. *J. Zool., Lond.* 167: 319-336.

GRAY, P.T.A. & P.J. MILL, 1983. The mechanics of the predatory strike of the praying mantid Hierodula membranacea. *J. exp. Biol.* 107: 245-275.

HEITLER, W.J., 1974. The locust jump. Specialisations of the metathoracic femoral-tibial joint. *J. comp. Physiol.* 89: 93-104.

OLESEN, J., 1972. The hydraulic mechanism of labial extension and jet propulsion in dragonfly nymphs. *J. comp. Physiol.* 81: 53-55.

OLESEN, J., 1979. Prey capture in dragonfly nymphs (Odonata, Insecta): Labial protraction by means of a multi-purpose abdominal pump. *Vidensk. Meddr dansk naturh. Foren.* 141: 81-96.

PARRY, D.A., 1983. Labial extension in the dragonfly larva Anax imperator. *J. exp. Biol.* 107: 495-499.

PRITCHARD, G., 1965. Prey capture by dragonfly larvae. *Can. J. Zool.* 43: 271-289.

PRITCHARD, G., 1976. Further observations on the functional morphology of the head and mouthparts of dragonfly larvae (Odonata). *Quaest. ent.* 12: 89-114.

RITZMANN, R.E., 1974. Mechanisms for the snapping behavior of two alpheid shrimp, Alpheus californiensis and Alpheus heterochelis. *J. comp. Physiol.* 95: 217-236.

ROEDER, K.D., 1959. A physiological approach to the relation between prey and predator. *Smithson. misc. Coll.* 137: 287-306.

SNODGRASS, R.E., 1954. The dragonfly larva. *Smithson. misc. Coll.* 123: 1-38.