

## THE ELICITATION OF THE PREDATORY LABIAL STRIKE OF DRAGONFLY LARVAE IN RESPONSE TO A PURELY MECHANICAL STIMULUS

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### SUMMARY

The predatory labial strike of dragonfly (*Aeschna*) larvae could be elicited by an artificial water jet stimulus.

The larvae showed fair prey-catching ability even when visually deprived, whereas when deprived of mechanosensory and visual information, the ability decreased sharply. Also, immobilized prey were unable to elicit a strike even from intact larvae.

The percentage of labial strike (PLS) increased in proportion to the logarithm of the water velocity at the body surface. Animals starved for 1 day or more showed higher PLS than satiated ones.

In addition to the water velocity, the movement of the jet nozzle (temporary change in the velocity) was also important in eliciting the labial strike. Although repetitive stimuli resulted in a rapid habituation of the labial strike, the second stimulus in a series was always the most effective: an arousal state to the newness was observed.

The anterior parts of the body surface (including the legs) showed higher sensitivity of PLS to the water jet stimulus, whereas the posterior parts elicited responses other than the labial strike: turning, head orientation and the setting of a posture.

These results explain nocturnal predation of larvae and predation in turbid pond beds where visual cues will be unavailable.

### INTRODUCTION

The larvae of the dragonfly *Aeschna* catch their prey by means of a well developed labium. The labium is ordinarily folded under the head. In predation it is protruded forward by internal body pressure and the labial palpi seize the prey. In the case of *Aeschna* larvae, it takes 25 ms for the labium to reach its full extension. The hydraulic mechanics have been described by Tanaka & Hisada (1980).

*Aeschna* larvae have large compound eyes. It has therefore been supposed that visual information plays a considerable role in predation (Baldus, 1926), and it is true that the labial strike of *Aeschna* larvae can be released by visual stimuli: Etienne (1968, 1969) demonstrated that a light spot with flicker or with zigzag motion is

effective for labial strike elicitation and that the image of the prey itself is not necessary. In addition to the visual cue, however, the animal must use other sensory capacities, because there is evidence of nocturnal feeding activity (Corbet, 1962), and the animals live in turbid pond beds.

In this paper we discuss the stimulation of the predatory labial strike of *Aeschna* larvae by chemical and mechanical senses.

#### MATERIALS AND METHODS

Larvae of the dragonflies *Aeschna nigroflava* Martin and *Aeschna juncea* Linne were used at their final stage of development. They were collected from various ponds near Sapporo. The habitats of the animals were sometimes in clear water, sometimes in turbid water. They were kept in water at 17–20°C, and fed with *Tubifex* sp. The two species and their sexes were not distinguished in the experiments because of no discernible difference in their prey-catching behaviour. The animals were starved for 1–11 days before the experiments (cf. Fig. 4).

The water jet was delivered into the water from a nozzle made of plastic tubing (Fig. 1). The strength of the jet was controlled by the nozzle size, the water head ( $h$  in Fig. 1) and the distance of the nozzle from the animal. The jet was turned on and off by a solenoid valve (US-M5-37, Chukyo Denki). Because it was impossible to measure the water velocity with sufficient spatial resolution, i.e. 1 mm, the line velocity of the water stream which actually stimulates the animal was estimated from the volume flow of water through the nozzle. Further details of the hydrodynamics used for the calculation of velocity distribution are presented in the Appendix. The sites of stimulation were tarsi on either side of the animals because it was easy to keep the distance from the nozzle constant. The nozzle was mounted on a magnet-vibrator (G-1, Fukuyou Onkyo) to give a horizontal sweep motion to the stimulus jet. A function-generator (G-502, Eisho Denshi) provided sine wave signals which were fed into the vibrator. The stimulus jet swept back and forth over the tarsal surface with a stroke distance of 4 mm. The stimuli were delivered to a single tarsus for a given number of stimuli, or during given time intervals. The labial strike was visually examined and the stimulus to which the response occurred was scored. The percentage of labial strike (PLS) was calculated as an average of the score for all six legs and for a group of test animals, unless otherwise noted. A group consisted of 10–30 individuals. Inter-stimulus intervals between application to each leg was more than 1 min. No learning about the 'emptiness' of the water jet stimulus was observed.

Visual deprivation was achieved by painting the eyes with black opaque lacquer. Mechanosensory deprivation was added by painting the six legs and antennae with lacquer. Other parts of the body surface were left intact. The experiments on the visually deprived animals were performed in a dark room under a red photographic safety light for the sake of double assurance. Tadpoles of *Rana chensinensis* (about 15 mm in body length) were presented as a model of the natural prey. The frog eggs were collected from the same ponds from which the *Aeschna* larvae were obtained. The number of prey captured or killed was continually replenished, so that the number of prey in the test arena was kept constant throughout the test. The test arena was a styrol chamber 8 cm in diameter and 4 cm in depth.

## RESULTS

*Sensory cues for the release of the predatory labial strike*

To ascertain the crucial sense which *Aeschna* larvae utilize for the release of predatory labial strike, the prey-catching ability of the animal was measured in intact animals, blinded animals and animals that were both blinded and lacked mechanosensory input (see Materials and Methods).

The number of tadpoles caught within 5-min spans was scored (Fig. 2). For the first 30 min, the tadpoles presented were immobilized with CO<sub>2</sub>. The immobilized tadpoles were not struck even by the intact animals. When the immobilized tadpoles were replaced with intact swimming ones, the larvae started to prey upon the tadpoles. The intact animals caught the largest number of prey. The visually deprived animals also showed a high ability for prey capture; especially at the beginning of the exposure to the swimming tadpoles, they had similar ability to the intact animals. In contrast, the animals deprived of both visual and mechanosensory cues showed a low ability for prey capture.

The intact larvae continued their prey strike even after satiation: the animals struck

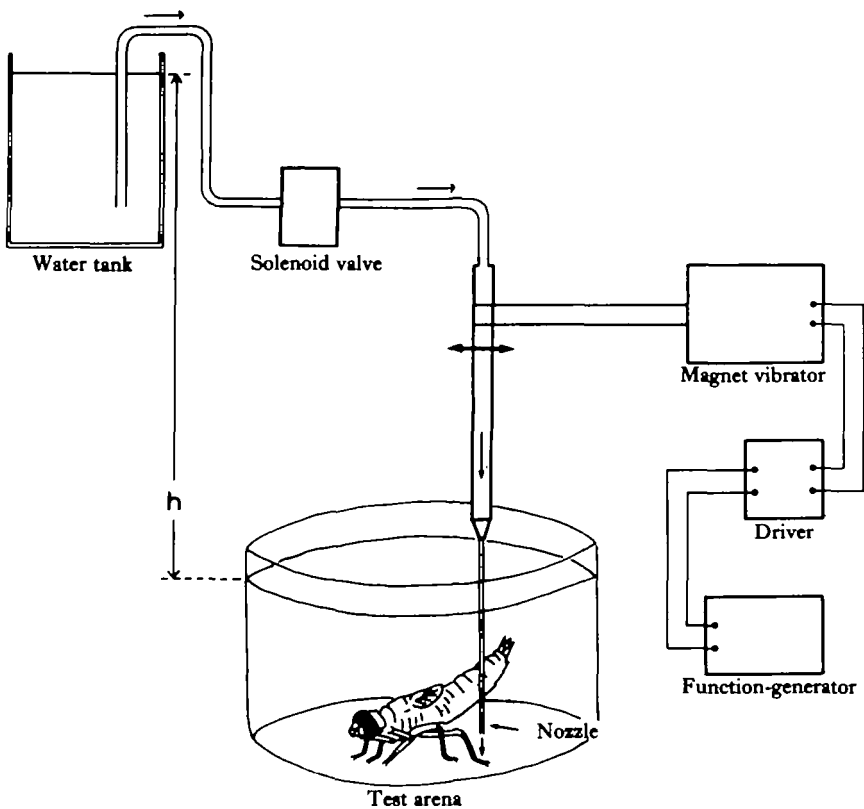


Fig. 1. The stimulatory equipment. The water was guided from a tank to the nozzle along polyethylene tubing through a solenoid valve. The nozzle moved back and forth so that the water streamed across the tarsus. The intensity of the jet was controlled by changing the water head ( $h$ ).

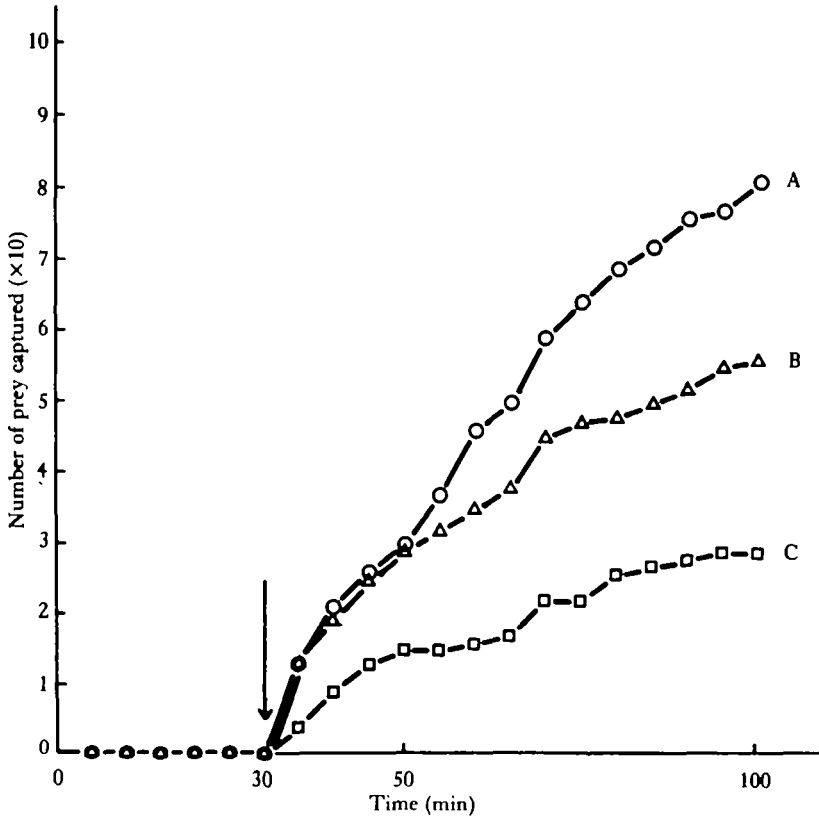


Fig. 2. Effects of sensory deprivation on prey-catching ability. (A) intact, (B) blinded and (C) blinded and deprived of mechanosensory hairs on antennae and legs. The arrow indicates when the immobilized tadpoles were replaced with intact ones. Total scores of 10 animals. The animals were starved for 7 days.

and killed their prey but no feeding occurred. This seemed to be a playful game invoked by the moving stimuli. The visually deprived animals also showed this non-feeding prey catch at a lower rate. The doubly deprived animals did not indulge in this kind of behaviour; their behaviour was limited to the catch and feeding.

We thus find that chemical senses are not involved in the labial strike because the immobilized tadpoles were not struck at all. The mechanosensory cues received by the legs and antennae appear necessary to enable a high performance of the predatory labial strike.

#### *The labial strike to water jet stimulus*

Since mechanical stimulation had been proved to be effective in eliciting the labial strike, a water jet was employed as a quantitatively controllable stimulus. When a jet of water was swept across the tarsal part of the larval leg, the animal made a labial strike towards the vicinity of the leg.

The percentage of labial strike (PLS) was first measured with respect to the jet velocity at the nozzle (Fig. 3, dashed lines). The stimulus jet swept a tarsus at a rate

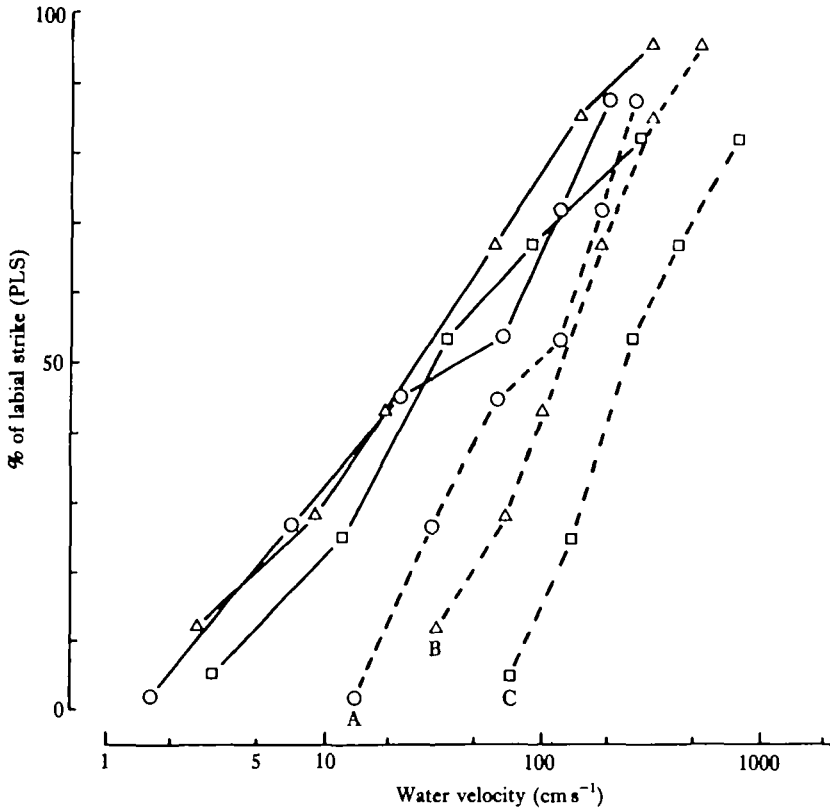


Fig. 3. Percentage of labial strike (PLS) to the water jet stimulus. Abscissa: the line velocity of water on a logarithmic scale. Results obtained from three different-sized nozzles are superimposed. (A) Open circles, 390  $\mu\text{m}$ ; (B) open triangles, 195  $\mu\text{m}$ ; (C) open squares, 100  $\mu\text{m}$ . Dashed lines, PLS plotted against the water velocity at the nozzle; solid lines, PLS replotted with respect to the estimated water velocity at the tarsus. Averaged for 10 animals.

of  $15\text{ s}^{-1}$ . The labial strikes elicited during 10 stimuli were counted. If the water stream was stationary, the animal showed only a low rate of labial strike (cf. Fig. 5). The PLS rose with the line velocity of the jet at the nozzle. In response to the high velocity jet the animal struck at the stimulus in more than 90% of the cases. The PLS curves were also dependent on the nozzle size, however. Three different-sized nozzles, with inner diameters of 100, 195 and 390  $\mu\text{m}$ , were used. A large nozzle gives a large momentum of fluid flow and therefore higher velocity at a distance, even for the same velocity at the nozzle (see Appendix). The PLS was therefore replotted with respect to the estimated velocity at the tarsus (Fig. 3, solid lines). Three such curves agreed well with each other. This indicates that the water velocity at the tarsal surface is the factor determining the PLS. The PLS rose linearly with the logarithm of the water velocity at the tarsus. Hereafter, the estimated value of water velocity at the tarsus is used as the stimulus quantity.

To determine whether the labial strike released in response to the water jet stimulus is a part of predation or part of some other response (e.g. defence), the effect of starvation on the PLS was measured (Fig. 4). Animals starved for 1–11 days showed

a consistently high PLS, whereas satiated animals (day 0) showed a high threshold and low PLS even to a strong stimulus. The labial strike in response to the water jet observed in the starved animal can therefore be seen as a part of predatory behaviour.

*The effect of sweep motion of the stimulus jet*

As mentioned in the previous section, the water jet must move across a part of the body surface of the animal to elicit the labial strike. The higher the rate of the sweep motion, the higher were the PLSs (Fig. 5). The water jet from a stationary nozzle was only effective at velocities of over  $100 \text{ cm s}^{-1}$  when turbulence may become significant (see Discussion). Because the stimulus jet swept the tarsal surface only once at  $1 \text{ s}^{-1}$  stimulus, whereas the jet at  $2 \text{ s}^{-1}$  gave 10 stimuli, these three curves are not directly comparable. Therefore the PLSs to a given number of stimuli at different rates were measured (Fig. 6). Although the first stimulus elicited a similar PLS irrespective of the repetition rate, the effectiveness of the subsequent stimuli depended on the repetition rate. At a high rate, all successive stimuli were effective to some extent (Fig. 6A). At a low repetition rate, the stimulus after the sixth presentation became ineffective (Fig. 6C). Thus the PLS depended on repetition rate, not number of stimuli. The

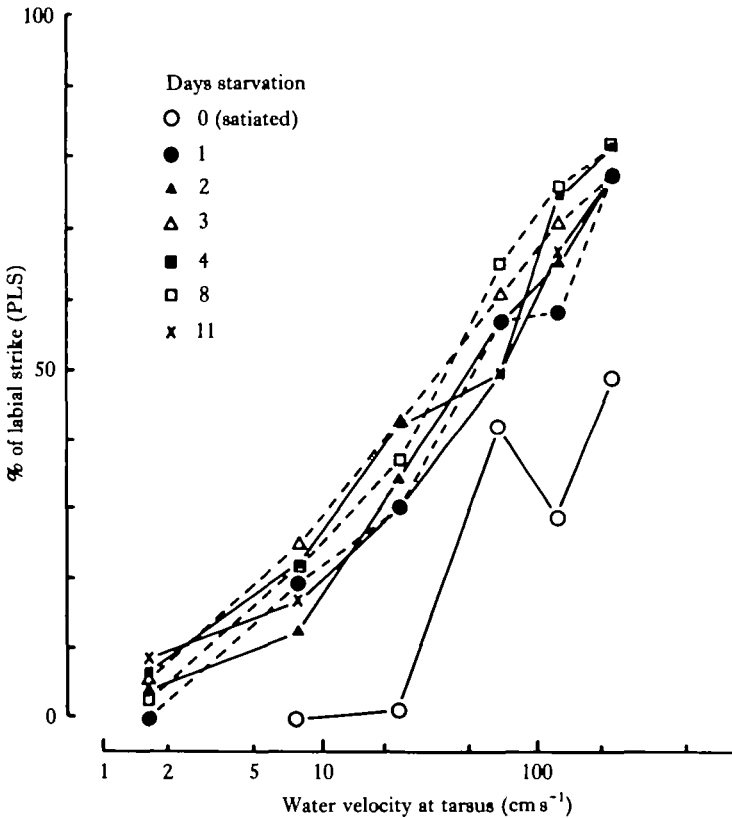


Fig. 4. Starvation period and the percentage labial strike (PLS). The nozzle-sweeping rate was  $0.1 \text{ Hz}$ . The labial strikes for 5 cycles were counted (one trial). PLS is the average for 12 animals, 6 legs per individual. After one day's starvation, the PLS rose. There is no significant difference between animals starved for 1–11 days.

time course for the increase of the PLS was clearly dependent upon the repetition rate (Fig. 7A). When the repetition rate of the stimulus was higher than  $1 \text{ s}^{-1}$ , the PLS rose quickly and reached a plateau. At the lower rate of  $1.5 \text{ s}^{-1}$ , the PLS reached a lower level of plateau with the slower rate of rise. These results are also true for the PLS to the weaker jet stimulus (dotted line in Fig. 7A).

Although the two PLS curves of the higher rate stimuli seem to fall in line with each other, the time course of the response probability to each stimulus differed (Fig. 7B). The responsiveness to each of the successive stimuli diminished quickly at the higher rate of stimuli, and slowly at the lower repetition. In addition to the difference in the 'adaptation rate', the responsiveness to the first stimulus also differed with the repetition rate. In the stimulus conditions employed here, the sweeping velocity of the nozzle was also affected when the repetition rate of the stimulus changed, because the stroking distance of the nozzle motion was constant. The difference of the responsiveness to the first sweep of the stimulus jet must be solely attributable to the sweep velocity. The nozzle swept at  $1.3$ ,  $6.5$  and  $13 \text{ mm s}^{-1}$  respectively at three repetition rates. The sweep rate of  $6.5 \text{ mm s}^{-1}$  seemed to be optimal in this situation (Fig. 7B).

The decrease in responsiveness to a successive stimulus, whose rate depends on the

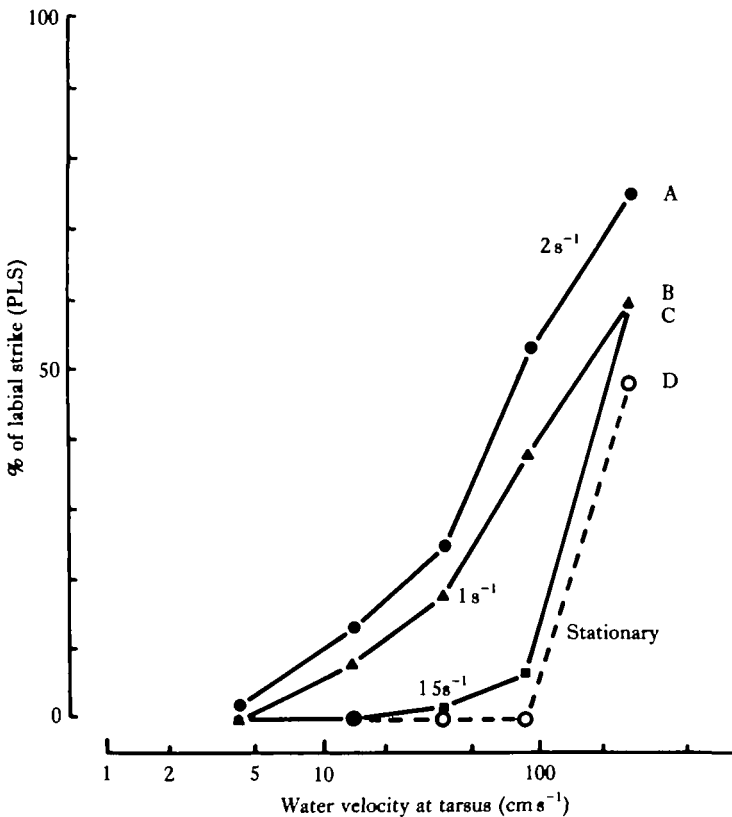


Fig. 5. The percentage labial strike (PLS) in response to the water jet with different sweep motions. The nozzle stimulated the tarsus at  $2 \text{ s}^{-1}$  (A),  $1 \text{ s}^{-1}$  (B),  $1.5 \text{ s}^{-1}$  (C) with a stroke distance of 4 mm. PLS was measured at intervals of 5 s. Average for 10 animals.

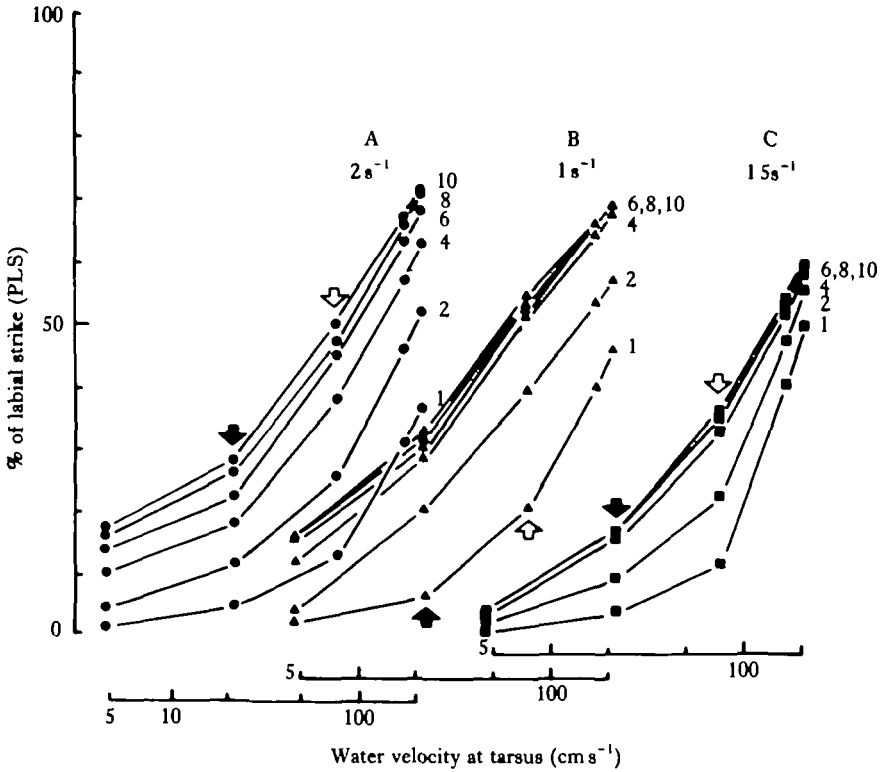


Fig. 6

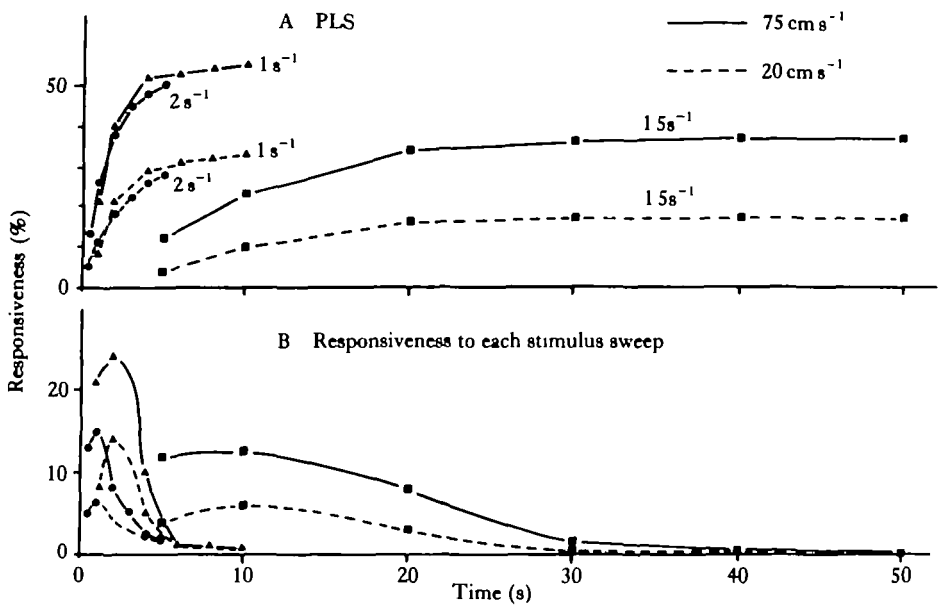


Fig. 7



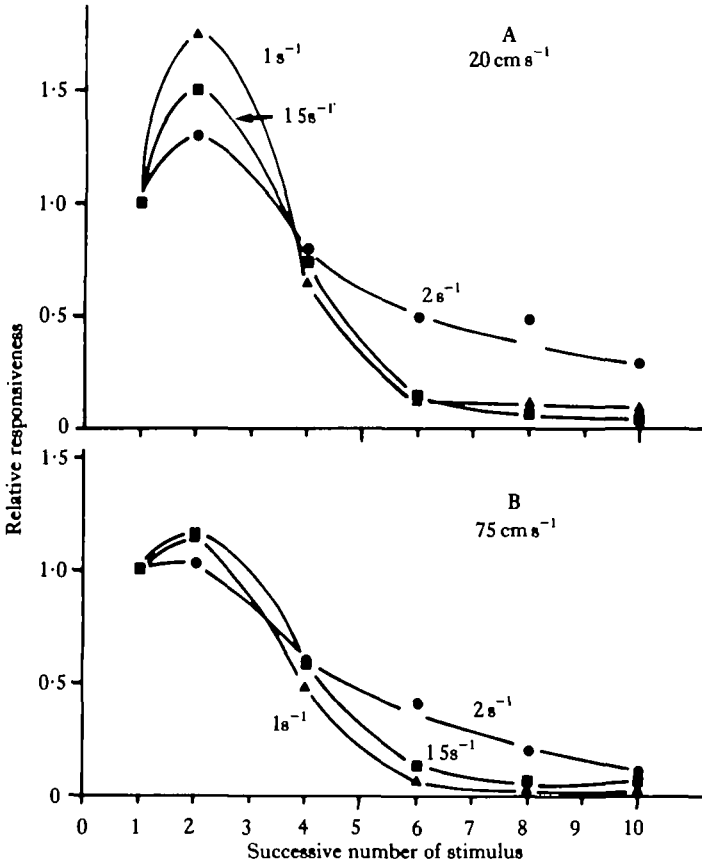


Fig. 8. Habituation processes during a succession of stimuli. Ordinates: responsiveness to each one of the successive stimuli normalized with that to the first one. The relative responsiveness changed with the successive number of stimuli given (abscissa) regardless of the variation of the repetition rates. Jet velocity: (A) 20 cm s<sup>-1</sup>, (B) 75 cm s<sup>-1</sup>. Replotted from Fig. 7B.

repetition rate of the stimulus, resembles the process of habituation. After normalization of responsiveness to the first stimulus, the responsiveness was plotted against the successive number of the stimulus (Fig. 8). Fig. 8 shows that the change in responsiveness was dependent on the number of experiences instead of the time elapsed or the repetition rate.

In addition to habituation during a succession of stimuli, the second stimulus always elicited a higher PLS than the first (Fig. 8). This facilitatory effect of the second stimulus therefore must be called the 'arousal' to the initial part of the

Fig. 6. Cumulative percentages of labial strike (PLSs) to the stimuli with different repetition rates. (A) 2 s<sup>-1</sup>; (B) 1 s<sup>-1</sup>; (C) 1.5 s<sup>-1</sup>. Each point indicates the PLS to the stimuli up to the given number, right ordinates. In (B) and (C), the stimuli coming after the sixth were ineffective, whereas the later stimuli can elicit the response in (A). Solid and open arrows indicate the stimulus intensities chosen for further analysis (see also Figs 7 and 8). Each point is an average for a group of 30 animals and 6 legs per animal.

Fig. 7. (A) The time course of percentage labial strike (PLS) during repetitive stimuli at various rates. (B) Response probability to each one of successive stimuli at various rates. Replotted from Fig. 6. The solid and the dashed lines correspond to the solid and open arrows in Fig. 6 respectively.

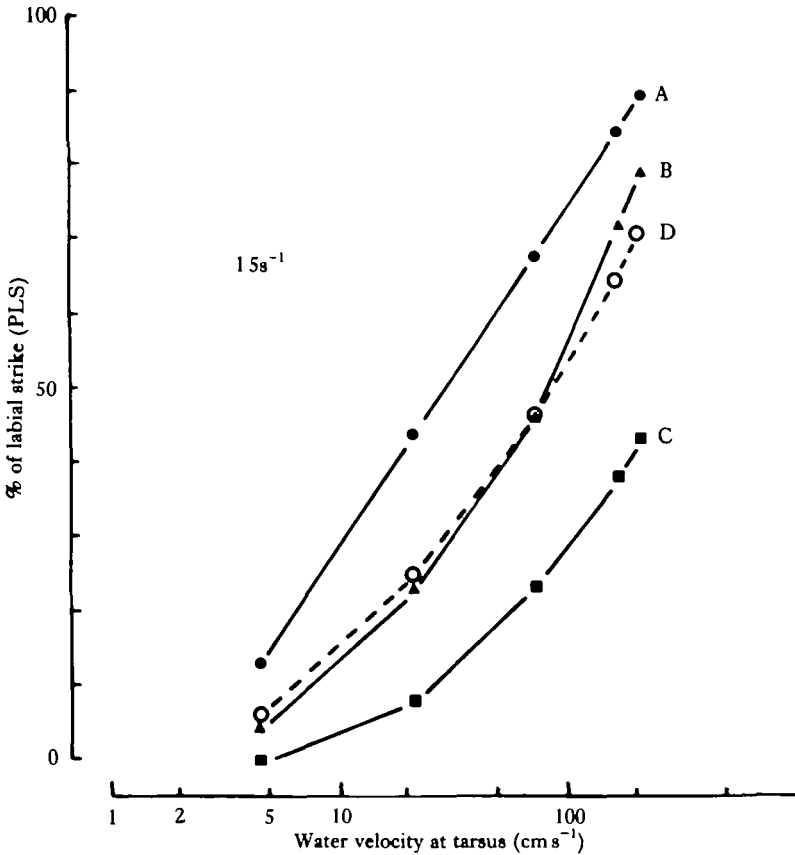


Fig. 9. Comparative sensitivity gradients of legs. The percentage of labial strike (PLS) was measured for five cycles of nozzle motion at the rate of one stimulus per 5 s. Averaged for both side legs and for 30 individuals. (A) Fore legs, (B) middle legs, (C) hind legs, (D) total.

successive stimuli. At the highest repetition rate, temporal summation of the stimulus was observed in addition to habituation and the arousal.

#### *Sensitivity gradient on legs*

Application of the water jet to the anterior part of the animal elicited the labial strike more effectively than stimulation of other parts (Fig. 9). Stimulation of parts distant from the head elicited behaviour other than a labial strike. Caudal stimulation elicited head orientation and turning of the whole body toward the stimulus. This behaviour may help the animal to collect more detailed information about the stimulus.

### DISCUSSION

#### *Principal cue for the predatory strike of Aeschna larvae*

The sensory deprivation experiment indicates that *Aeschna* larvae can utilize the mechanosensory capacity as well as the visual one for the predatory strike. Normal animals in daylight may use visual stimuli as mentioned by previous authors (Baldus,

1926; Etienne, 1968, 1969). Pritchard (1965) demonstrated that the size and motion of the prey are important for dragonfly larvae in recognition of prey, while shape, colour and odour are not. This agrees well with the apparent feeding behaviour of dragonfly larvae: they appear to eat only small living animals. Even after the mechanosensory functions of the antennae and the legs are deprived, dragonfly larvae still have the ability to prey, although it is low. This indicates that the mechanoreceptors on the body surface are able to locate the source of mechanical disturbance.

Paulian & Serfaty (1944) reported that the larvae of *Aeschna cyanea* have the habit of nocturnal wandering. The same behaviour has been reported for *Anax imperator* (Corbet, 1962). Corbet (1962) thought that nocturnal wandering was for feeding. The predation of dragonfly larvae must therefore greatly rely upon mechanosensory information other than visual. Our present observations suggest that *Aeschna* larvae use mechanical senses as primary cues in their prey-catching behaviour.

Although the effective quantity of the stimulus jet is the line velocity at the body surface of the animal, there will also be fluctuation of velocity. The undulatory body motion of the swimming animal produces a series of water movements in which water is ejected backwards. This ejected water would give a wave of velocity change to the surroundings. Sensory capacities to mechanical waves have been reported in some aquatic insects, for example whirligig beetle (Reinig & Uhlemann, 1973), water strider (Murphey, 1971*a,b*), and back swimmer (Wiese, 1972, 1974; Murphey & Mendenhall, 1973; Murphey, 1973). These insects use surface wave motion as signals for prey-location. In the case of the back swimmer, the mechanoreceptive hairs at the tip of the abdomen are important for the orientation behaviour (Murphey & Mendenhall, 1973). *Aeschna* larvae have filiform sensory hairs, greater than 500  $\mu\text{m}$  in length on the cuticular surface. The sensory hairs are rich on the legs and antennae. The sensory hairs associated with the prey-catching ability will be reported elsewhere (Y. Tanaka, M. Kanou & M. Hisada; in preparation).

Repetition rate of an artificial mechanical stimulus affects the PLS. However, sequential analysis reveals that the animal shows quick habituation. In contrast to habituation, an arousal state is triggered by the first stimulus, ensuring a high responsiveness to the second stimulus. This type of attention and habituation mechanism must underlie the discrimination mechanism of the living prey.

#### APPENDIX

The line velocity of a water stream caused by a jet was calculated as follows.

Supposing  $u(y,r)$  expresses the line velocity along the axis of the cylindrical coordinates, the velocity distribution at the nozzle is parabolic along the radius (Fig. 10A),

$$u(0,r) = \frac{V_0}{a^2} (a^2 - r^2), \text{ (cm s}^{-1}\text{)},$$

where  $a$  is the inner radius of the nozzle,  $V_0$  is the maximum velocity of the jet at the nozzle. The volume flow  $Q$  is therefore:

$$\begin{aligned}
 Q &= \int_0^a 2\pi r u dr \\
 &= \int_0^a 2\pi r \frac{V_0}{a^2} (a^2 - r^2) dr \\
 &= \frac{\pi}{2} V_0 a^2
 \end{aligned} \tag{1}$$

We measured  $Q$  directly and then calculated  $V_0$  for a given condition of water head for each individual nozzle.

According to Schlichting (1979), the stream pattern caused by a jet is given by a solution of the Navier-Stokes differential equation. For the sake of theoretical simplicity, an ideal jet whose line velocity at the nozzle is infinity is supposed. The ideal jet is ejected to water through an infinitesimally small orifice, and has a definite value of kinematic momentum  $K$ . The kinematic momentum  $K$  of the jet characterizes the streamline of the water. The kinematic momentum of the real jet is given by an integral of momentum at a small part.

$$\begin{aligned}
 K &= \frac{1}{\rho} \int_0^a \rho u \cdot u \cdot 2\pi r dr \\
 &= 2\pi \int_0^a u^2 r dr \\
 &= \frac{\pi}{3} V_0^2 a^2 \quad (\text{cm}^4 \text{s}^{-2}),
 \end{aligned} \tag{2}$$

where  $\rho$  is the density of water,  $\rho u$  is a mass of water injected through an area at radius  $r$ . The axial and radial velocity components,  $u$  and  $v$  respectively, are given by Schlichting (1979)

$$\begin{aligned}
 u &= \frac{3}{8\pi} \cdot \frac{K}{vx} \cdot \frac{1}{(1 + 1/4 \xi^2)^2} \\
 v &= \frac{1}{4} \cdot \sqrt{\frac{3}{\pi}} \cdot \frac{\sqrt{K}}{x} \cdot \frac{\xi - 1/4 \xi^3}{(1 + 1/4 \xi^2)^2} \\
 \text{where } \xi &= \sqrt{\frac{3}{16\pi}} \cdot \frac{\sqrt{K}}{v} \cdot \frac{r}{x}
 \end{aligned}$$

and  $\nu$  is the kinematic viscosity of water (about  $0.01 \text{ cm}^2 \text{ s}^{-1}$  at  $20^\circ \text{C}$ ).

At the centre of the jet axis, the water velocity achieves its maximum,

$$u(x,0) = \frac{3}{8\pi} \cdot \frac{K}{0.01} \cdot \frac{1}{x} \quad (\text{cm s}^{-1}). \tag{3}$$

Thus, the velocity at the centre of the jet attenuates with distance. By using a  $u$  denotation, the axial component of the water velocity along the radial distance is represented as:

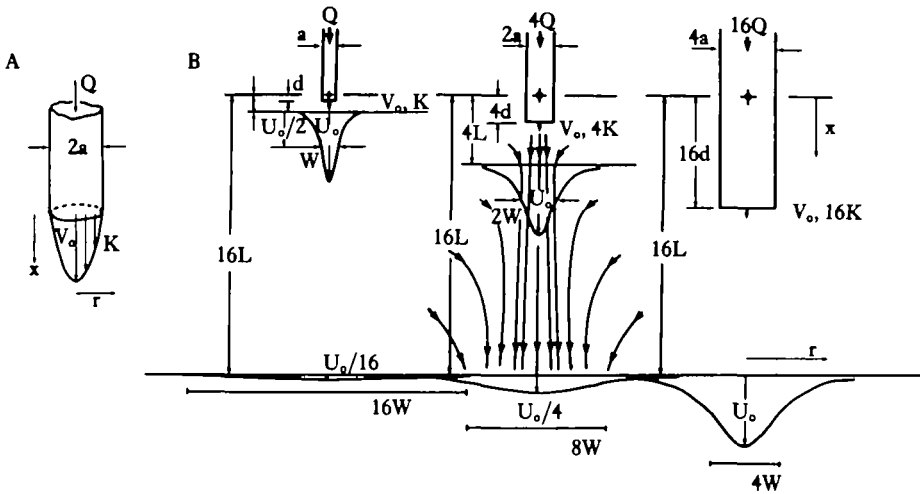


Fig. 10. Stream line of the water caused by a jet. (A) Parabolic distribution of velocity at the nozzle and the coordinates system. (B) The axial component of the water velocity. For the same  $V_0$ , different-sized nozzles give the different kinematic momenta which characterize the stream line of the water.  $a$ , Nozzle diameter;  $d$ , correction distance of the ideal jet orifice;  $L$ , distance from the ideal orifice;  $U_0$ , line velocity at the centre of the jet;  $W$ , the half width of the stream at a distance;  $K$ , kinematic momentum;  $Q$ , volume flow.

$$u(x, r) = \frac{u(x, r)}{[1 + 149 \cdot 2K (\frac{r}{x})^2]^2} \quad (\text{cm s}^{-1}). \quad (4)$$

As the stimulus quantity, the maximum velocity at the tarsi was chosen. For example, suppose nozzle size of  $a$  was  $50 \mu\text{m}$ ,  $V_0$  calculated from equation (1) was  $320 \text{ cm s}^{-1}$ , and the distance from nozzle to tarsi was  $0.5 \text{ cm}$  (Fig. 10). Therefore  $K$  is calculated as  $2.7 \text{ cm}^4 \text{ s}^{-2}$  from equation 2. From equation 3, the ideal jet orifice whose  $K$  is  $2.7 \text{ cm}^4 \text{ s}^{-2}$  and which causes  $V_0$  of  $320 \text{ cm s}^{-1}$ , should be postulated at a distance of  $0.1 \text{ cm}$  behind the real nozzle. This is a correction distance 'd' indicated as  $d$  in Fig. 10B. Then the water velocity at  $0.6 (= 0.1 + 0.5) \text{ cm}$  from the ideal jet whose  $K$  is  $2.7$  was again calculated from equation 3. The water velocity estimated is thus  $53 \text{ cm s}^{-1}$ . The radial distribution of water velocity at a distance from the nozzle is calculated by equation 4 and is expressed in Fig. 10 employing various values of  $K$  for comparison.

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