ON THE DORSAL LIGHT RESPONSE IN A MAYFLY NYMPH

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Introduction

The dorsal light response orientates the animal in such a way that light is kept perpendicular to both long and transverse axes of the body (Fraenkel & Gunn, 1940). It maintains or contributes to the maintenance of the animal's normal primary dorso-ventral orientation in its natural environment.

This response has been reported in a number of swimming invertebrates including Ephemeroptera nymphs (v. Buddenbrock, 1915). Other records include *Palaemon xiphias* (Decapoda) (Alverdes, 1926); *Argulus foliaceus* (Copepoda) (Herter, 1927): *Daphnia* (Cladocera) (Schulz, 1928): *Triops* (Eubranchiopoda) (Seifert, 1930): *Hirudo medicinalis* (Hirudinea) (Schluter, 1933): *Arcilius* and *Dytiscus* (Dytiscidae) (Schone, 1951): and *Corixa* (Corixidae) (Rabe, 1953).

Ventral light reflexes in which the animal maintains itself with its ventral surface towards the light have been recorded in *Chirocephalus* and *Artemia* (Eubranchiopoda) (Seifert, 1932) and in *Notonecta* (Notonectidae) (Rabe, 1953).

Nymphs of the baetid, *Baetis harrisoni* Barnard showed varying degrees of 'somersaulting' (Fig. 1) within a horizontal light beam (Hughes, 1966). These nymphs were apparently disequilibrated by the absence of a dorsal orienting stimulus and the reflection of light off the white painted substrate. The existence of a dorsal light response was therefore tested in the following experiments.

Fig. 1. Diagrammatic representation of the somersault executed by *Baetis harrisoni* (vertical aspect).

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Methods and Results

'Somersaulting' in the light beam virtually ceased in the ultimate nymphal instar whereas in the penultimate instar and all earlier stages it was of frequent occurrence. The amount of 'somersaulting' varies in different individuals but it appeared that most individuals were consistent in the amount that they carried out. This was verified by selecting individuals which showed no somersaulting and those which frequently did, and subjecting these individuals to successive trials within the light beam and plotting their tracks (Fig. 2); the somersaults are indicated by loops in the tracks. There is clearly a consistency in the amount of somersaulting incorporated into the movements of individual nymphs over a period of at least several hours.

Experiment 1

Four glass dishes (A, Fig. 3) were placed on a sheet of glass (B), and half-filled with water (4 cm in depth). Two 40 W lamps (C and C) were placed 20 cm above and 20 cm below the dishes and their light diffused through opal glass (D). (The light intensity incident on the glass dish was approximately 1000 ft-candles.) The nymphs were divided into four categories: (i) ultimate instar, (ii) penultimate instar, (iii) middle stages from approximately the twelfth to the sixteenth instar, and (iv) early stages from approximately the fourth to the eighth instar. Twenty nymphs of each category were placed in separate dishes. Under alternate conditions of top and bottom lighting, five series of readings were taken of the number of nymphs which were lying on their dorsal surface in each dish. This was the criterion whereby disequilibrium was measured (Fig. 4).

The results for the ultimate nymphal instar have been examined statistically using Student's t test, and it was found that the difference between the numbers disequilibrated by a top and by a bottom light was significant ($t=4\cdot6$; $P<0\cdot001$), but was much less significant than that for the early, middle and penultimate instars ($t = 18\cdot8$; $24\cdot8$ and $22\cdot9$ respectively).

Nymphs of *Baetis harrisoni* in slow water currents in the absence of a current repeatedly release their hold on the substrate and swim
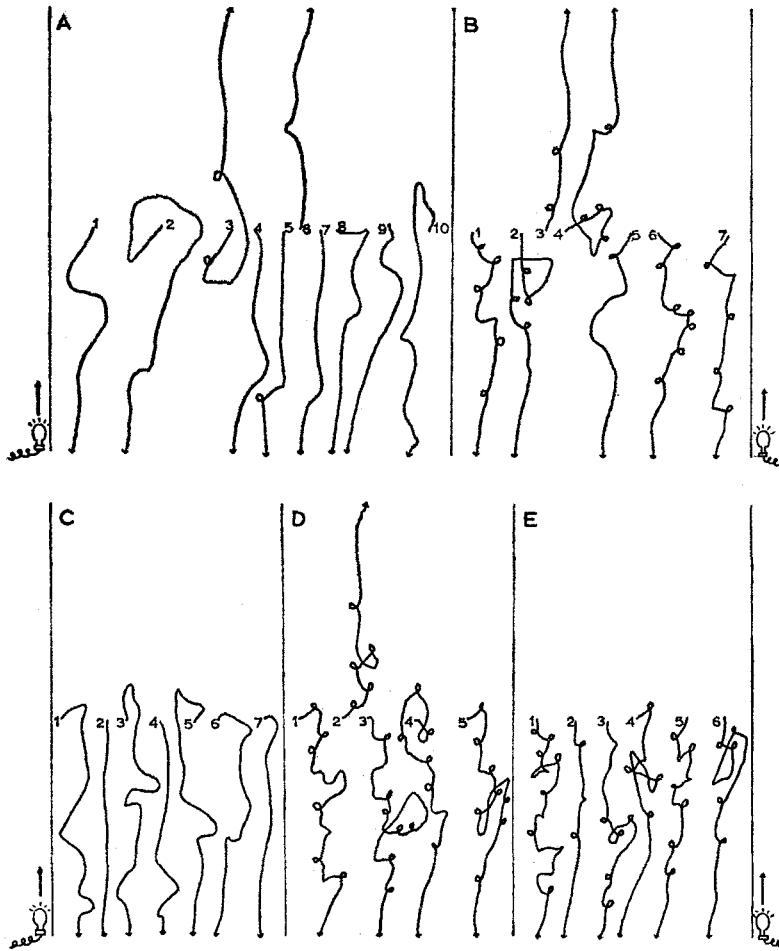
Fig. 2. Consecutive tracks of five middle stage nymphs of *Baetis harrisoni* within a light beam. A consistency in the degree of somersaulting is shown by individuals.
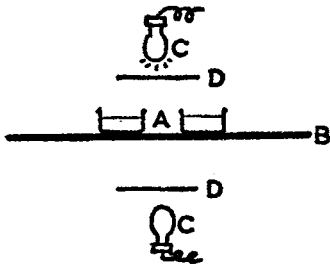

Fig. 3. Diagram of apparatus to investigate dorsal light response (vertical section) (details in text).

upwards towards the surface of the water; at varying heights above the substrate they stop swimming and fall back. This activity may serve to create a current over the integument. In other mayflies this current would normally be created by gill movements, but the latter are absent in the Baetidae. When carrying out this type of movement nymphs would sometimes turn on their backs either momentarily only or would sink back to the substrate dorsal surface downwards.

Experiment 2

Four glass dishes were placed below a 40W lamp so that they were equally illuminated through opal glass. Two dishes were placed on a white sheet of paper and two on black. Ten middle stage nymphs were placed in each dish and counts were made of the number in each
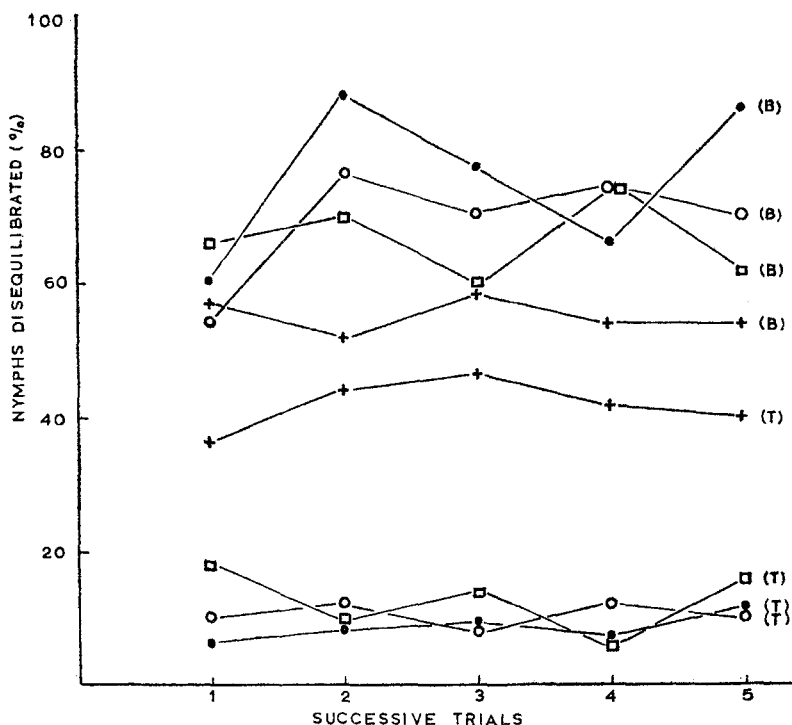
Fig. 4. The percentage disequilibration of four different stages of the nymphs of *Baetis harrisoni* when exposed to alternate top (T) and bottom (B) light sources, each point being the mean of five trials each with twenty nymphs. +,ultimate instar; □, middle stages; ○, penultimate instar; ●, early stages.

which, during twenty 5-sec periods, turned on their dorsal surfaces.

The total number of nymphs which turned upside down in the two dishes placed on a white sheet was 237/400 or 59 per cent and in the two dishes placed on a black sheet 45/400 or 11 per cent.

Discussion

It is evident (Fig. 4) that the position of the light source has a very marked influence on the maintenance of the primary dorso-ventral orientation of the penultimate instar, middle and early stages of *Baetis harrisoni* nymphs. In the ultimate instar however the direction of light is operative as an orienting stimulus only to a limited degree and the effect on the dorso-ventral orientation is small.

The fact that the final nymphal instar, unlike the other instars, does not 'somersault' within the light beam and that this final instar does not exhibit the same strong dorsal light response as the other three categories examined, supports the hypothesis that the 'somersault' can be

accounted for in terms of a dorsal light response.

The extent to which this response is effective in the maintenance of equilibrium is shown in experiment 2 in which a white substrate was sufficient often to disorientate nymphs severely even in the presence of a high intensity of light from above. This response is undoubtedly of great importance to the swimming nymph and is possibly the sole means of determining its dorso-ventral position. In the case of non-swimming nymphs the dorsal light response can be overridden by a substrate which can easily be grasped; indicating that normal orientation, when not swimming, is probably maintained principally by other position receptors such as leg proprioceptors and tarsal touch receptors. This has been shown to be the case in *Palaemon xiphias* (Alverdes, 1926, 1928) and *Corixa* and *Notonecta* (Rabe, 1953). In the former the stato-cysts and tarsal touch receptors, and in the latter two species the antennal proprioceptors, can effectively override the orientating effect of the dorsal or ventral light response.

The significance, if any, of the loss of this

response by the ultimate instar is not obvious, neither is the mechanism of the sudden change. De Ruiter (1962), investigating the ontogenetic change in light orientation in eyed hawk caterpillars (*Smerinthus ocellata* L.), showed that this shift was probably due to endocrine changes. In this case however there is not a gradual shift, but a very abrupt change in the ultimate instar. This sudden absence of response may be the result of the observed opaqueness of the cuticle covering the ocelli just prior to the emergence of the sub-imago. This assumes that the ocelli are the receptors mediating the dorsal light response. Although it has been previously shown (Herter, 1927 in *Argulus*; Alverdes, 1926 and 1928 in *Leander xiphias*; Schone, 1951 in *Acilius* and *Dytiscus*) that balanced stimulation of the light receptors is necessary for the maintenance of the normal posture through the dorsal or ventral light response, Seifert (1930) has shown that in *Triops*, which has two compound eyes and a median eye on the dorsal surface, the latter communicating with a 'window' on the ventral surface, the reaction is initiated by the median eye and only maintained thereafter by balanced stimulation of the two compound eyes.

It is postulated that in *Baetis harrisoni* similarly, the dorsal light response is initiated by the ocelli and maintained tropotactically by the compound eyes. The ocelli in the final instar are only semi-transparent to light, and therefore only a very small response is elicited. As the thickness of the cuticle over the ocelli will vary with respect to the time of ecdysis, this viewpoint also offers an explanation for the marked differences in the extent of 'somersaulting' carried out by different nymphs of what are apparently the same instar (Fig. 2).

The disorientation caused by the absence of an overhead light source and the inability of nymphs to 'land' efficiently on the substrate having sunk back upside down after their short upward swims, point to the probable explanation for the phenomenon of drift in at least some running water forms. Elliott (1965), in laboratory experiments, confirmed field results which indicated a greater drift by night than by day. The number of *Baetis* spp. in drift were 618 by night and 73 by day.

The absence of the orienting light source by night coupled with the greater degree of activity exhibited by nymphs of several species of mayfly at night (Harker, 1953) would account for the above figures for drift.

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