laboratory experiments on *Zenarchopterus* to be reported elsewhere; they demonstrate polarotactic behaviour patterns quite distinct from the menotactic orientation observed in the field.

To understand the interaction of such polarotactic and menotactic orientation[9], field experiments must be carried out at various times of day with different geographical Sun's bearings. Pre-sunrise and post-sunset experiments might isolate the influence of natural *e*-vector patterns from the direct effect of the Sun's rays, but further study would be required of the anomalous submarine polarization patterns known to be present at dusk[8,10,11].

The question of the mechanism of *e*-vector perception in a teleost is intriguing. It has been suggested that extraocular dichroic structures might provide the necessary analyser (personal communication from T. Kuroki, 1968), yet the fresh skin and skull over the midbrain region of *Zenarchopterus* where there is a translucent "window" do not show significant dichroism which might modulate a pineal or neighbouring midbrain photoreceptor.

Fishes, of course, lack rhabdoms whose specific fine structure relative to the orientation of visual pigment chromophores underlies polarized light sensitivity in arthropods and cephalopods[9,12–17]; nor do they have the macula lutea thought to be responsible for Haidinger's brushes in man.

At the suggestion of Dr Gary Bernard of the Yale Ophthalmology Department we are investigating the possibility that twin cones, which are of unknown function but occur in the retinas of a number of teleosts[18,19], might provide an analyser mechanism. Although the fine structure of their receptor membrane is quite different from that of a rhabdom their ordered arrangement in rectangular or oblique patterns in certain fishes[20] is strikingly reminiscent of the regular mosaic of rhabdomeres and rhabdoms of arthropod compound eyes[21]. Thus far light microscopic sections of *Zenarchopterus* retina prepared in collaboration with Mrs Mabelita Campbell have shown that twin cones are prominently present in regular array. It remains to be shown whether they may provide any basis for *e*-vector discrimination. Experiments to test this are in progress with Dr Haruo Hashimoto.

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Retention of a Conditioned Avoidance Response after Metamorphosis in Mealworms

METAMORPHOSIS of holometabolous insects involves extensive reorganization of their nervous systems[1,2]. In spite of such changes, behavioural modifications can be demonstrated at the adult level after manipulations in the larval stage[3–5]. For example, the adult reactions of *Nemeritis* and *Drosophila* to chemical cues have been altered by exposure to these cues during the larval stage[3,4]. One limitation of these experiments, as Thorpe points out, is that the behavioural modification cannot be assessed directly in the larval stage. Using a more formal conditioning procedure, Borrell du Vernay[5] found that *Tenebrio* trained to discriminate between surfaces and thus avoid shock in the larval stage showed subsequent savings in relearning the discrimination as adults. Unfortunately, this study did not include controls for such variables as sensitization to shock and familiarization with the test situation.

We report here an unambiguous demonstration of retention though metamorphosis. The first of our two experiments showed that either larval or adult *Tenebrio molitor* L. could learn a passive avoidance task; the second demonstrated that responses learned by larvae persisted in adults.

The training chamber in both experiments was a uniformly illuminated lucite box 5 × 7·5 cm in size. The floor was divided into two parts: one with a lucite surface and the other with a copper surface. Copper wires, 7 mm apart, were suspended 1 mm above the copper surface. When an insect bridged the space between the wires and the underlying copper surface, it received shock until it returned to the lucite surface. Insects, selected randomly from stock culture, were isolated for at least 7 days and then individually introduced on to the lucite (safe) surface. The interval between introduction to the lucite surface and the first movement to the copper surface was termed the response latency; an increase in response latency during successive days of training was a measure of learning. Each daily session ended when an insect remained on either surface for 30 min. Fig. 1 summarizes the results from our first experiment. On day 1, for both larvae and adults, the copper surface was not electrified, thereby providing a measure of the preferences of untrained insects. The latency of the first response (from lucite to copper) did not exceed 200 s for larvae or 40 s for adults—all animals had a pretraining preference for the copper surface; the adults and larvae spent 89 and 89·5 per cent respectively of the total time in the chamber on the copper.

On subsequent training days (days 2–6 for larvae and days 2–7 for adults) the copper surface was electrified. As Fig. 1 shows, the latency of the first response increased significantly during training. This increase, however, need not represent only passive avoidance conditioning, but it could be attributed in part to habituation effects or to the fact that the animal sampled shock without actually crossing to the copper surface. During the next 2 days we investigated these alternatives.

On the day after training, no shock was given, but both larvae and adults remained on the lucite surface for the full 30 min (Fig. 1): apparently sampling did not account for the increase in response latency observed during training. Each animal was then left in the apparatus until it had explored both surfaces and remained on

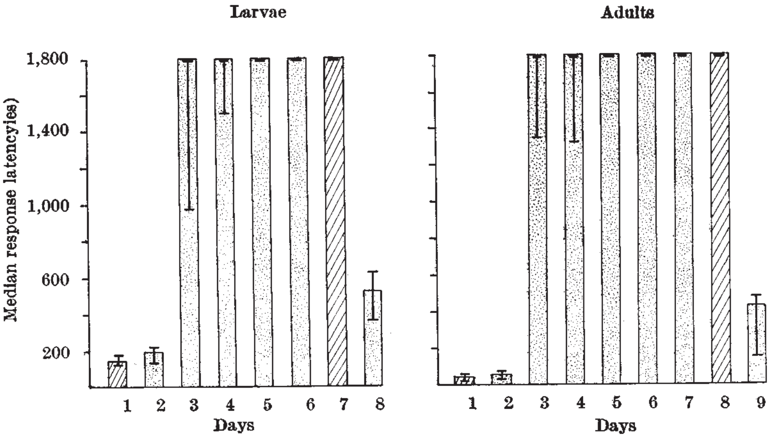

Fig. 1. Median response latency for the first movement of larval and adult *Tenebrio* from lucite to copper surface. Interquartile intervals are indicated by brackets. Ten animals comprised each group. Stippled columns, copper surface electrified; hatched columns, copper surface not electrified.

one of them for 60 min. On the next day, the copper surface was electrified again, and response latencies decreased sharply (Fig. 1). Because the pattern of preference built up during training had been reversed by 1 day without shock, habituation to the lucite surface could not possibly explain the increase in response latencies during training. It is most probable that increased latency reflects true conditioning.

Our second experiment involved the same training procedure, but each animal was trained as a larva and tested as an adult. Control groups were used to determine the degree to which conditioning, habituation, sensitization and/or familiarization in the training sessions with larvae contributed to the behavioural modifications following metamorphosis. One experimental and two control groups were used. The experimental group (trained) consisted of larvae that were trained for at least 10 days, allowed to pupate and tested for retention 3 days after the adult moult. One control group (no treatment) consisted of larvae that were allowed to explore the testing apparatus in the absence of shock, allowed to pupate and tested as adults. The other control group (non-contingent shock) consisted of larvae that were exposed to non-contingent shock in the training chamber, allowed to pupate and then tested as adults. In the non-contingent shock procedure, larvae were exposed to shock-on and shock-off for approximately the same periods of time as were larvae in the trained group, but a lucite barrier prevented movement; they were transferred from one surface to the other by hand.

Retention in adult beetles was measured by two criteria: (1) duration of first period on the safe surface (avoidance latency), and (2) number of errors before the beetle remained on the safe surface for 30 min (trials to learn). On both indices (Table 1), the trained group performed significantly better than either of the control groups: relative to the controls, the trained group showed longer avoidance latencies ($P < 0{\cdot}01$) and fewer trials to learn ($P < 0{\cdot}01$). (The Mann–Whitney U two-tailed test was used.)

Persistence of behavioural modification through a moult is not a new idea, as indicated by previous studies[3–6]. Our present study has shown that neither sensitization nor habituation explains retention following a moult. It is more significant that persistence of a specific conditioned response survives the extensive reorganization of the central nervous system during the pupal stage. Implicit in these data, and in need of further investigation, is the probability that storage of information occurs in specific portions of the central nervous system which retain their integrity through the pupal and imaginal moults.

Table 1. MEDIAN AND INTERQUARTILE RANGE OF AVOIDANCE LATENCY (S) AND TRIALS TO LEARN IN ADULT *Tenebrio* PREVIOUSLY TRAINED IN THE LARVAL STAGE

Group	n	Avoidance latency		Trials to learn	
No treatment	25	41 (33–49)		3 (2–4)	
			} $P < 0{\cdot}01$		} $P < 0{\cdot}01$
Conditioned	25	1,800 (1,800–1,800)		0 (0–0)	
			} $P < 0{\cdot}01$		} $P < 0{\cdot}01$
Non-contingent	31	83 (15–204)		3 (2–4)	

In either larva or adult, learning to avoid aversive situations is of obvious advantage to the individual insect; certainly such behavioural plasticity would be favoured by natural selection. In this kind of learning, the general exploratory tendencies of the insect are inhibited by a set of learned clues. The fact that the inhibition persists not only within a single instar but also across the pupal stage suggests that each adult will tend to remain in the area which was most favourable for its own larval growth. Thus adult habitat preferences are biased by larval experience. This "place learning" is a conservative phenomenon, reinforcing the isolation of those local populations which are concentrated within the more favourable niches of a heterogeneous environment. Place learning could play a part parallel to and/or complementary with the preimaginal conditioning reported by Thorpe and Jones[3].

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Note added in proof. Shortly after we submitted this manuscript, an article on learning in *Tenebrio* by Borsellino and his co-workers[7] came to our attention. In contrast to our passive avoidance procedure, the Borsellino study used maze learning; it was satisfying to find that retention over metamorphosis occurred with both types of conditioning.

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Rhythmic Patterns in Human Interaction

Now that the importance of rhythmicity in biological behavioural functions has been recognized, the traditional distinctions between psychology and physiology have had to be reappraised. For example, the regular alternation between mania and depression in manic-depressive psychosis suggests the possibility of underlying rhythmic phsyiological mechanisms[1]. Similarly, the temporal structure of social interaction has been investigated and regular patterns have been found[2]. Chapple[3] and others[4] have suggested a loose analogy between these patterns and biological rhythms. Nobody, however, has analysed the temporal structure of interaction with the perspective and statistical techniques of chronobiologists.