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AN ENDOGENOUS CREPUSCULAR RHYTHM OF RAINBOW TROUT (*SALMO GAIRDNERI*) PHOTOMECHANICAL MOVEMENTS

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SUMMARY

1. The position of the epithelial pigment and cones in the retina of *Salmo gairdneri* was determined during extended periods of darkness in fish entrained to both artificial and natural light/dark cycles.

2. An endogenous rhythm of such photomechanical movements, unique among species so far examined, was observed in both groups of fish, with two peaks of light adaptation coincident with dawn and dusk.

3. It is suggested that such an apparently non-adaptive physiological rhythm is related to the behavioural pattern of trout and reveals a basic crepuscular organisation.

4. No endogenous rhythm was observed in continual light.

5. These results suggest that control of photomechanical changes in rainbow trout has two components: an endogenous component, that causes the bimodal pattern in maintained darkness, and a direct effect of light, that maintains light adaptation throughout a normal day.

INTRODUCTION

Photomechanical (retinomotor) responses are the movements of the retinal epithelial pigment (R.E.P.) and visual receptors in response to ambient lighting conditions. In the dark-adapted state, the epithelial pigment aggregates at the back of the eye, the cones expand to take up a position near Bruch's membrane in close proximity to the pigment epithelium, and the rods are contracted near the external limiting membrane (E.L.M.). In response to light the cones contract to take up a position near the E.L.M., completely surrounded by the R.E.P. The rods, which exchange places with the cones, are buried in the R.E.P. near Bruch's membrane.

Although these movements were first described nearly a century ago (Arey, 1915; Detwiler, 1943; Ali, 1971, 1975, for reviews), they have been little investigated in recent times and certain aspects of their function are, as yet, unclear. One question that has been investigated repeatedly, however, is whether such retinal migrations have an endogenous rhythmic component.

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Previous work has shown that fish kept in continual light are always fully light adapted, no matter what the time of day, but some form of persistent endogenous retinomotor rhythm during extended periods of darkness has been reported in six species of fish (Welsh & Osborn, 1937; Arey & Mundt, 1941; John & Haut, 1964; John, Segall & Zawatsky, 1967; Olla & Marchioni, 1968; John & Gring, 1968; John & Kaminester, 1969; Wagner unpublished), and an internal rhythm may be the cause of 'irregularities' in the behaviour of cones of two further species when subjected to darkness during normal daylight hours (Nicol, 1965). There have, however, also been several reports of these movements failing to occur when fish have been subjected to extended periods of darkness (Ali, 1959, 1961; Wagner & Ali, 1977). Although Wigger (1941) is often quoted as having shown a persistent rhythm in goldfish, *Carrasius auratus*, this is not the case. The fish were fully dark adapted 4 h after sunset, after which the retinal elements started to migrate toward their light-adapted positions, until after 12 h in the dark they took up a position intermediate between light and dark adaptation. This position was maintained for the remaining 50 h of the experiment. Thus it seems that in some species photomechanical movements have an endogenous component, while in others they do not.

The present study reports an endogenous rhythm in rainbow trout, which is worth describing for several reasons. Firstly, Ali (1959, 1961) and Wagner & Ali (1977) have reported that retinomotor rhythms do not occur in several species of salmonid, and salmonids as a whole are therefore widely quoted as not possessing an endogenous photomechanical rhythm. This is not substantiated by the present results. Secondly, the form of rhythm found in rainbow trout is totally different from any pattern previously reported. Thirdly, it is felt that most earlier studies, although adequate to demonstrate a rhythm, may not be detailed enough to reveal the exact pattern of such movement. Finally, the results may help to explain the different forms of endogenous retinomotor rhythms found in various species.

MATERIALS AND METHODS

Dissection, fixation and measurement

The fish used in this study (9–14 cm) were obtained from the Howietoun fish farm, Bannockburn.

Dissection and fixation were carried out in dim red light. Fish were removed from the experimental situation and immediately killed by a sharp blow on the head. The eyes were excised from the orbit and the complete eye, punctured at the corneal/scleral junction to facilitate penetration, was immersed in Bouin's fixative for at least 24 h. Following fixation the eye was removed under normal lighting conditions, hemisected, and a square of retinal/scleral tissue removed from around the base of the optic nerve. This ensured that a similar area of the eye was always sampled from different individuals, which is of importance as different parts of the retina may show differing degrees of migration or pigmentation (e.g. Hess, 1910; Fujita, 1911; Wunder, 1925; Kobayashi, 1957).

Subsequently, the tissue was washed in distilled water, dehydrated in D.M.P. (acidified 2:2 dimethoxypropane, Muller & Jacks, 1975) and embedded in Emix resin

Sections 2–5 μm in thickness were then cut on an LKB pyramitome and stained with 1% Toluidine blue in a 1% Borax solution.

The state of adaptation of the eye was expressed using both cone and pigment indices. No measurements on the rods were made as they could not be distinguished by the present histological procedure. The cone index is taken as the distance between the E.L.M. and the base of the cone ellipsoid, divided by the distance between the E.L.M. and the basement membrane. Similarly, the pigment index is the distance between the basement membrane and the outermost projection of the pigment, again divided by the distance between the E.L.M. and the basement membrane.

One section was obtained from anywhere within the above mentioned area and at least two regions sampled, one either side of the optic nerve, with at least five cone measurements and one pigment measurement being made in each region. More readings were made in eyes that were dark adapted or in an intermediate state of adaptation, as cone positions in such sections are more variable than in light-adapted eyes. To compensate for variation between individuals, wherever possible at least three fish were sampled at any one time. Different cone types were not distinguished. By sampling from a large number of fish, and from several locations within each section, any differences in retinomotor movements of different cone types that may be present (e.g. Walls, 1942; Müller, 1954; Engström & Rosstrop, 1963; Nicol, 1965; John *et al.* 1967; Olla & Marchioni, 1968) should be averaged out. All measurements were made with the experimenter ignorant of the exact lighting conditions the eye being measured had been exposed to, thus controlling for any possible observer bias.

Experimental design

The existence of a retinomotor rhythm was investigated using both fish adapted to the natural light/dark cycle (Expts 1–3) as well as fish entrained to an artificial laboratory light regime (Expts 4–8).

Initially the behaviour of the retinal elements throughout a natural 24 h period was determined. Fish, which had been exposed to the natural light/dark cycle for at least a year, were collected from the fish farm during the afternoon, put in a large tank outside away from any artificial lighting, and then sampled during the following dusk and dawn periods (Expt 1).

Subsequently, in Experiments 2 and 3, fish were treated in a similar manner, except that after the end of the dusk period at 22.00 h the fish were transferred, in total darkness, to blacked out tanks in the laboratory and sampled at intervals thereafter. Fish were also sampled throughout the natural fall in illumination prior to being put into darkness so as to ensure that they were dark adapting normally and that factors such as stress from the journey had in no way affected the retinomotor movements.

In Expts 4–8, on the other hand, fish were transferred from the fish farm to the laboratory and entrained to artificial light/dark cycles for varying periods. On arrival in the laboratory the fish were kept for several weeks in an aquarium, and fed daily on trout pellets. Subsequently, they were adapted in 75 × 45 × 40 cm tanks supplied with running water (16–17.5 °C). These tanks were covered by a lid containing fluorescent lights (650 lux at water surface) which, coupled to a timer, supplied a 12 h light/dark cycle (09.00–21.00 h or 07.00–19.00 h).

Table 1. *Conditions under which rainbow trout (Salmo gairdneri) were kept and subsequently sampled in 8 retinomotor rhythm experiments*

(The symbols d and n indicate that the fish were held under natural illumination; the symbols L and D indicate that the fish were held under artificial illumination.)

Experiment	Number of fish	Experimental conditions		When sampled
		Light regime	Duration	
1	56	Natural d/n	Over a year	At dawn and dusk
2	54	Natural d/n	Over a year	In dark, over 24 h
3	199	Natural d/n	Over a year	In dark, over 96 h
4	16	12 h L/12 h D	15 days	During L/D cycle
5	8	12 h L/12 h D	7 days	In dark, over 35 h
6	20	12 h L/12 h D	14 days	In dark, over 41 h
7	20	12 h L/12 h D	29 days	In dark, over 28 h
8	32	12 h L/12 h D	25 days	During constant L

In Expt 4, which is analogous to Experiment 1 for naturally entrained fish, fish were sampled during an actual laboratory light/dark cycle. For Expts 5–7 the lights were permanently turned off at 'dusk' of the last day of adaptation, and fish sampled beginning around the following 'dawn'. Conversely, in Expt 8 the lights were left on after the last day of entrainment and fish sampled throughout the following night.

Table 1 summarizes all experiments carried out. Times of sampling can be ascertained from the individual figures.

RESULTS

The positions of the retinal elements during a natural 24 h period are shown in Fig. 1. Movement of the retinal elements from the dark to the light-adapted position and the reverse migration can be seen to occur at the same time and with the same speed as the natural changes in illumination.

Fish subjected to continual darkness, after having been exposed to the natural light regime, were not always dark adapted as would be the case if there was no endogenous control of retinal element movement. In Expt 2 there are two peaks of light adaptation occurring around what would normally have been dawn and dusk (Fig. 2) had the light cycle been maintained. During the dawn period the retinomotor movements follow the outside change in illumination exactly, behaving identically to fish actually exposed to such conditions (Fig. 1). The second peak occurs about 2 h after the level of illumination started to fall in nature. Expt 3 investigated the longevity of this rhythm (Fig. 3). Unfortunately, two fish were sampled on only five occasions during the first day in darkness, as it was anticipated the results would be the same as in Expt. 2. The times sampled should have shown the peaks observed in the previous experiment, but failed to do so. Two very distinct peaks of light adaptation did, however, occur on the second day in darkness, indicating that the pattern is present. From this and from the experiments outlined below, it seems reasonable to suppose that the peaks were there on the first day of Expt 3, but were missed due to infrequent sampling. After the second day in darkness the pattern became more erratic.

When the eyes in Expt 3 were classified as either light adapted, dark adapted or intermediate, depending on their indices (Table 2), a chi-squared test showed that the

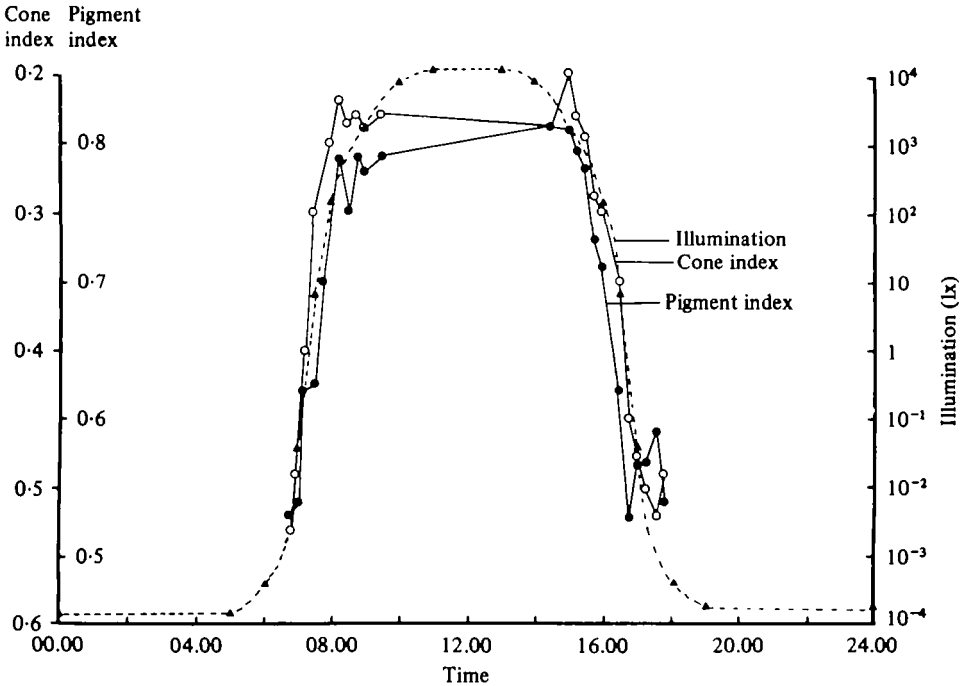


Fig. 1. Retinal pigment (●) and cone (○) indices during consecutive dawn and dusk periods (Expt 1). Each point during dawn is the average of two fish, while each point during dusk is the average of three fish. (▲---▲), Level of illumination.

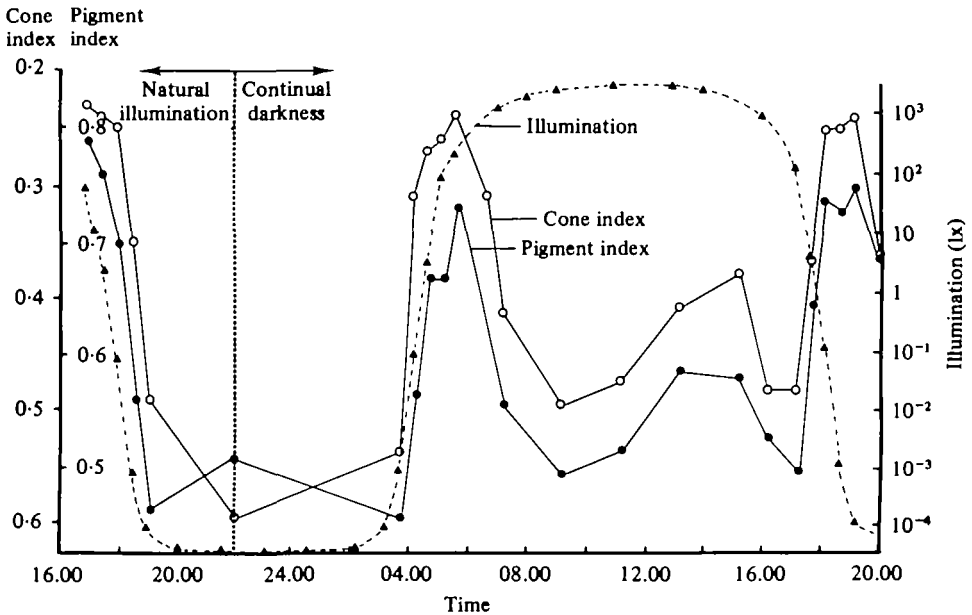


Fig. 2. Retinal pigment (●) and cone (○) indices in naturally entrained fish during 24 h darkness (Expt 2). Each point during the natural dusk represents one fish while all others are the average of three fish, except at 18.00, 19.00, 19.30 and 21.00 when only two fish gave suitable sections. The dashed line (▲---▲) is the level of illumination (lx) outdoors during the period when the fish were in darkness in the laboratory.

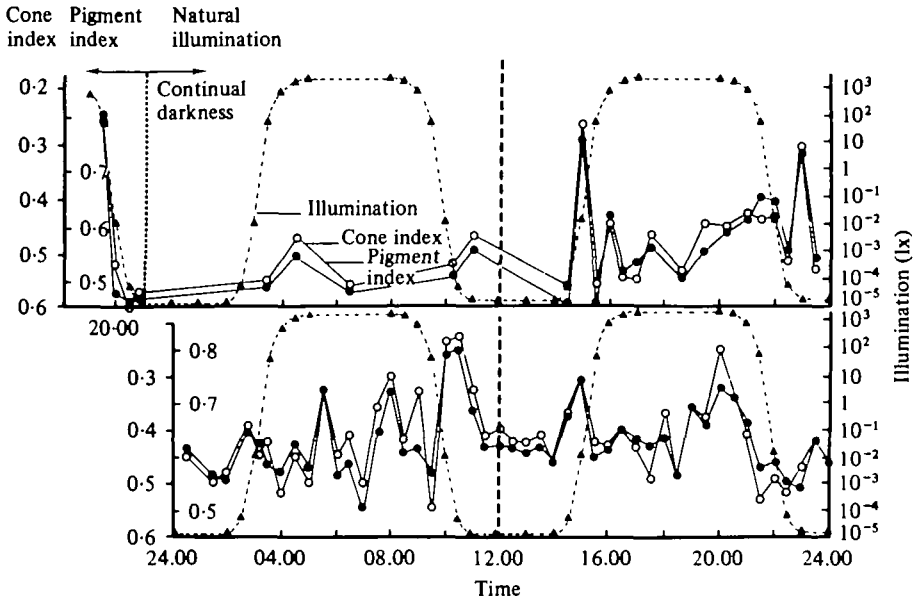


Fig. 3. Retinal pigment (●) and cone (○) indices in naturally entrained fish during 98 h darkness (Expt 3). Each point during the natural dusk represents one fish, each point during the first day is the average index value of two fish, while all other points are the average values of three fish, except 10.00 and 19.00 on day two and 01.00, 06.00 and 18.00 on day four which are the averages of two fish. The dashed line (▲---▲) is the level of illumination (lx) outdoors during the period the fish were in darkness in the laboratory.

Table 2. *Proportion of rainbow trout (Salmo gairdneri) whose eyes are in one of three states of adaptation on the second, third and fourth days in darkness (Expt 3)*

Light-adapted eyes have pigment indices (P.I.) > 0.79 and cone indices (C.I.) < 0.3. Dark-adapted eyes have P.I. < 0.6 and C.I. > 0.45. Eyes in an intermediate state of adaptation have P.I. = 0.6–0.75 and C.I. = 0.3–0.45.

Day	Proportion of eyes light adapted (%)		Proportion of eyes in an intermediate state of adaptation (%)		Proportion of eyes dark adapted (%)		Total number of fish
	P.I.	C.I.	P.I.	C.I.	P.I.	C.I.	
2	11	11	22	22	67	67	46
3	20	26	37	33	43	41	70
4	9	15	61	48	30	37	69

proportion of eyes in these three categories of adaptation varied with time in the dark (pigment index, $P < 0.001$; cone index, $P < 0.01$). The relative number of fish whose cones and pigment were in an intermediate state of adaptation increased the longer the fish had been in darkness, while the proportion of eyes fully dark adapted decreased. The number of light-adapted eyes showed no systematic variation with time. Thus on the whole, the longer the fish are subjected to darkness, the more eyes are found in an intermediate state of adaptation at the expense of dark-adapted eyes.

Expts 2 and 3 were carried out 6 months apart, at times when the declination of the sun was zero. This ensured that the time and rate of change of natural illumination

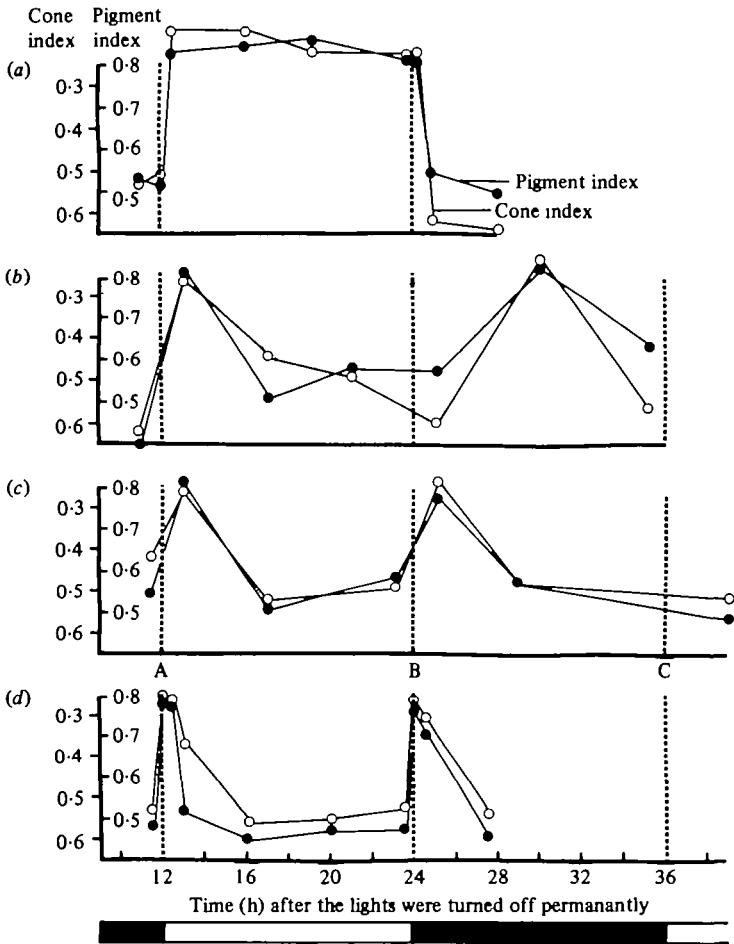


Fig. 4. Retinal pigment (●) and cone (○) indices in various lighting conditions following laboratory adaptation to a 12h light/dark cycle. (a) Expt 4, fish sampled in a maintained cycle. Each point is the average index value of two fish. (b) Expt 5, fish sampled in darkness after 7 days entrainment to the light/dark cycle. Each point represents one fish, except 25 h after the lights were turned off which is the average of two fish. (c) Expt 6, fish sampled in darkness after 14 days entrainment to the light/dark cycle. Each point is the average of three fish, except the last point which is the average of two. (d) Expt 7, fish sampled in darkness after 29 days entrainment to the light/dark cycle. Each point is the average index value of two fish. A is the time at which the lights would come on had the cycle been maintained. B and C mark the times at which subsequent changes in illumination would have taken place. The light and dark bars indicate the lighting conditions that would have prevailed had the light/dark cycle been maintained.

was the same in both cases, thus facilitating direct comparison between the two experiments. In both cases (Figs. 2, 3), the fish sampled during the dusk preceding the first experimental day of complete darkness showed normal retinomotor adaptation to the ambient light, indicating the journey had not significantly affected this process.

Results for the artificially adapted fish are summarized in Fig. 4. Fish sampled during the actual light/dark cycle (Expt 4) behaved as expected, being light adapted in the light and dark adapted in the dark. It is interesting to note that the eyes of fish

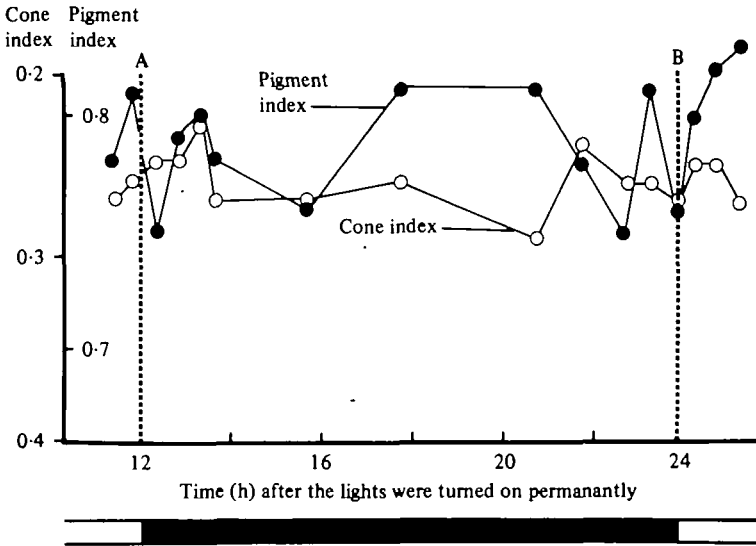


Fig. 5. Retinal pigment (●) and cone (○) indices of fish kept in continual light following twenty-five days entrainment to an artificial light/dark cycle (Expt 8). The average dark-adapted index values found in fish during an actual light/dark cycle are 0.58 and 0.52 for cones and pigment respectively. Each point is the average index value of two fish, except those at 09.30–11.30 which represent only one fish. (A, B) Previous times of lights off and on respectively. The light and dark bars indicate the lighting conditions that would have prevailed had the light/dark cycle been maintained.

sampled at light onset are not light adapted, indicating that these fish do not anticipate the lights coming on.

As in naturally entrained fish, those fish subjected to extended periods of darkness showed two distinct peaks of light adaptation (Fig. 4*b-d*). Fish adapted to the light/dark cycle for 7 and 14 days were fully light adapted 1 h after the lights would normally have gone on. The former also showed a second peak of light adaptation 6 h, and the latter 1 h, after the lights would normally have gone out at the beginning of the second night. Unfortunately, in neither experiment were fish sampled directly at the times when the lights formerly came on and off, as at the time the significance of these periods was not recognized. In Expt 7, however, the eyes of fish were examined at the previous times of lights on and off, and found to be fully light adapted at, and half an hour after these times, while during all other periods the eyes were totally dark adapted. It is possible that had fish been sampled at these times in Expts 5 and 6 they too would have been light adapted.

A superficial examination of Fig. 4(*b-d*) would seem to indicate that the dusk peaks become more synchronized with the actual time the lights would normally have gone off the longer the period of entrainment to the light/dark cycle. There are, however, not enough data points to allow one to state this with any certainty.

Finally, Fig. 5, which gives the results of Expt 8, shows that the retinal elements are in a light-adapted condition when kept in continual light (650 lx) no matter what the time of day, indicating the absence of a retinal rhythm in the light.

DISCUSSION

The results show that rainbow trout possess an endogenous retinomotor rhythm during extended periods of darkness, with two distinct peaks of light adaptation coincident with dawn and dusk. This rhythm lasts for two days and probably longer. If it were possible to follow the retinal movements of an individual over an extended period of time, it is likely that one would see the two peaks gradually losing synchrony with the natural changes in illumination. As there is no reason to suppose different fish will lose synchrony together, these peaks will be obscured by averaging the results of different fish. Over the first two days of darkness in Expt 3, light-adapted eyes were only observed in individuals sampled at the times when the peaks of light adaptation occurred, but on subsequent days light-adapted fish were found evenly distributed throughout the day. Individual fish might thus still be exhibiting the rhythm.

From Fig. 3 one can see that the average state of adaptation rises over the four days of Expt 3. This is partially caused by the loss of synchrony mentioned above, but is also due to the greater proportion of fish whose eyes are in an intermediate state of adaptation (Table 2). Such an increase in the number of semi-adapted, at the expense of dark-adapted, eyes indicates that this might be the relaxed state of the retina. This implies that the more complete dark adaptation during the first days in darkness both in naturally and laboratory entrained fish is an active process.

Previous workers have often kept fish in darkness for several days in order to break any endogenous rhythm and thus ensure total dark adaptation. It now seems, at least in the case of the trout, that this would be counterproductive, and that to ensure totally dark-adapted eyes naturally adapted fish should be used.

A comparison with the literature shows that the rhythm presented here is unique among those reported so far. The only results even remotely similar are those of John & Gring (1968), who noted greatest light adaptation at sunrise and sunset, and Wigger (1941), where light adaptation was again greatest at sunrise. However, it is quite possible that such a two peaked rhythm is not restricted to rainbow trout, but has been missed in other species due to infrequent sampling.

From previous studies it is tempting to extrapolate the results and conclude that some fish, in conditions of continual darkness exhibit retinomotor movements such as those found in fish under natural lighting conditions, as shown, for example, for trout in Fig. 1. However, such a conclusion, based on so few data points, may not be valid. Many of the earlier studies involved sampling only every twelve hours, and such infrequent sampling may lead to the true pattern of movement being obscured. The demonstration that fish sampled at noon are more light adapted than those sampled at midnight, although indicative of some form of rhythm, gives no information about, for example, the position of the retinal elements at dawn and dusk. Several reported demonstrations of a lack of such rhythms are also unsatisfactory for similar reasons (e.g. Ali & Anctil, 1977; Ali & Pickford, 1979).

All previous studies on rhythms have, however, revealed some degree of light adaptation in what would normally be the middle of the day, a situation very different to the present study. As John & Kaminester (1969) consider even the relatively small

differences in the rhythms of *Astyanax mexicanus*, *Carassius auratus* and *Lepomis macrochirus* to be attributable to species differences, it is likely that the unique pattern seen in rainbow trout is attributable to the same cause.

If true species variation does exist, an explanation for these differences must be sought. Several studies have established a correlation between the position of the retinal elements and certain behavioural phenomena (Olla & Marchioni, 1968; John & Gring, 1968; John & Haut, 1964; McFarland, Ogden & Lythgoe, 1979), so that John & Gring (1968) state: 'It would not be surprising to find that behavioural rhythms and retinomotor rhythms are commonly correlated in fishes.' Thus, it is possible that an explanation of the observed species differences in retinomotor rhythms may be found by examining the behavioural rhythms of the various species. Unfortunately, a search of the literature revealed no detailed studies of *Salmo gairdneri* behavioural rhythms. The only relevant data came from a laboratory study by Landless (1976), who demonstrated that rainbow trout, trained to demand feed, showed a correlation between feeding peaks and dusk. He also does not rule out the possibility that a dawn peak may have been present.

Studies on other salmonid species, especially the brown trout, *Salmo trutta*, however, are numerous. These studies have often revealed crepuscular peaks of activity (Holliday, Tytler & Young, 1974; Tytler *et al.* 1977; Young *et al.* 1972; Priede & Young, 1977; Oswald, 1978; Swift, 1962, 1964; Chaston, 1969; Bachman, Reynolds & Casterlin, 1979; Eriksson, 1973, 1978) and the evidence is summed up by Bachman *et al.* (1979): 'Notwithstanding considerable variation among individual experiments, the overall pattern emerging from the above studies is that activity peaks (in brown trout) tend to be associated with dawn and/or dusk, indicative of a crepuscular pattern.' This basic crepuscular behavioural pattern demonstrated in *S. trutta* correlates well with the endogenous crepuscular retinomotor rhythm found in the present study for *S. gairdneri*. It would of course be preferable to have similarly extensive behavioural data for *S. gairdneri*, but a comparison with *S. trutta* activity patterns should nevertheless be valid as the two species are closely related. If so, this would support the idea that retinomotor and behavioural rhythms are correlated.

However, such a two peaked retinomotor rhythm appears to be non-adaptive. It is reasonable that at dawn the retinal elements should move to their light-adapted position, and also that they should return to a dark-adapted position after encountering darkness, but to become light adapted again at dusk, when normally the elements would be dark-adapting, has no obvious function. Such a seemingly non-adaptive pattern can, however, be understood if one takes the viewpoint of Schwassman (1971), who considers that many of the overt rhythms are no more than the external manifestations of an internal circadian organization, and that by themselves they may have no adaptive significance. The twin peaks shown by the retinomotor movements of rainbow trout may thus be no more than the side effects of the fish's basic crepuscular organization.

At dawn the receptors are normally dark adapted. The movements are then triggered by the internal clock and the retinal elements change position. In nature this would be functional, but in the experimentally induced continual darkness the elements are in an inappropriate position for the lighting conditions, and therefore

return to the dark-adapted position. At dusk, in nature, these movements are once again set in motion, adapting the fish to twilight. In the artificial continual darkness the internal mechanism still continues to trigger a change in the position of the retinal elements, thus causing another peak of light adaptation, which, due to the maintained darkness, will once again be only transitory. The fact that in other studies the retinal elements remain in the light-adapted position throughout the day while the fish is exposed to continual darkness, may be due to a different, non-crepuscular, underlying timing mechanism. It would be interesting to see if other crepuscular fish show similar bimodal retinomotor peaks when maintained in darkness, and if such peaks ever occur in non-crepuscular species.

The control of photomechanical changes, at least in rainbow trout, can thus be thought of as consisting of two components: an endogenous component, that causes the bimodal pattern in maintained darkness, and a direct effect of light, that maintains light adaptation throughout a normal day. Such central control has been indicated, for instance, by the demonstration of an effect of hypophysectomy on photomechanical changes (Ali & Pickford, 1979), while a local effect of light has been demonstrated using small spot stimuli by Easter & Macy (1978) and with unilateral illumination by Ali (1964). A direct stimulating effect of light explains why fish remain light adapted and do not show any rhythm in continuous light (Fig. 5).

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