J. mar. biol. Ass. U.K. (1961) 41, 695–698
Printed in Great Britain

PHOTOMECHANICAL CHANGES IN THE EYES OF FISHES

I. RETINOMOTOR CHANGES IN *SOLEA SOLEA*

By J. A. C. Nicol
The Plymouth Laboratory

(Plates I and II)

In many vertebrates (except Mammalia) cellular movements take place in the pigment epithelium and receptor layer of the retina in response to changes of illumination. These movements, known as retinomotor changes, are especially well marked in teleost fishes. In fishes exposed to light, the retinal pigment moves outwards towards the external limiting membrane, the cone myoids contract causing the cones to shorten towards the light, and the rod myoids elongate causing the rods to extend away from the light. Reverse changes take place in dim light and darkness. These responses are characteristic of fishes living in illuminated waters. Cited exceptions are eels, in which the cones are static, and flatfish, in which only the pigment moves whereas rods and cones are stationary (Garten, 1907; Parker, 1932; Bayliss, Lythgoe & Tansley, 1936; Walls, 1942). The present investigation deals with the pattern of retinomotor changes in the common sole *Solea solea* (L.).

MATERIALS AND METHODS

Soles were held in a tank of circulating sea water at 15° C. The room was light-proof and the tank could be illuminated by two 100 W bulbs directly overhead (distance 0·7 m). Soles were placed in the tank in the evening and lights were turned on next day, if desired. At the conclusion of the experiment fish were decapitated, corneas were pricked, and the heads were dropped into Bouin's solution. Eyes were sectioned in celloidin or wax and were stained with haematoxylin and eosin plus Biebrich scarlet. Sections were cut dorso-ventrally, through the centre of the eye. Bleaching was carried out with potassium permanganate followed by oxalic acid.

At least three fish were used for each experiment. Experiments were as follows:

(1) Dark-adapted. In dark 16.30–09.30 h. 17 h in darkness.
(2) Dark-adapted. In dark 17.00–12.00 h. 19 h in darkness.
(3) Dark-adapted. In dark 17.00 h (first day) to 24.00 h (second day). 31 h in darkness.

(4) Dark-adapted. In dark 17.00–06.00 h. Illuminated $8\frac{1}{2}$ h, 06.00–1430 h. Then treated:

(*a*) darkness $\frac{1}{2}$ h, 14.30–15.00 h.
(*b*) darkness 1 h, 14.30–15.30 h.
(*c*) darkness, 2 h, 14.30–16.30 h.

(5) Light-adapted. In darkness 16.30–09.30 h. Then treated:

(*a*) illuminated $\frac{1}{2}$ h, 09.30–10.00 h.
(*b*) illuminated 1 h, 09.30–10.30 h.
(*c*) illuminated 2 h, 09.30–11.30 h.

When a pigment index is used it has the following significance: 1, pigment basal, fully retracted; 2, $\frac{1}{4}$ expanded; 3, $\frac{1}{2}$ expanded; 4, $\frac{3}{4}$ expanded; 5, fully expanded (or extended).

OBSERVATIONS

Retinal pigment

Dark-adapted eyes. The retinal pigment was partially or wholly retracted in fish which had been in darkness (Pl. I, fig. 1).

(1, 2, 3) Darkness 17, 19, 31 h. The pigment was wholly or largely withdrawn into basal regions of the cells. Dorsal and central retina, index 1. In the ventral retina it was sometimes partially expanded (indices, 1, 2, 3). There was no difference between animals killed at 12.00 h and 24.00 h.

(4*a*) Darkness $\frac{1}{2}$ h. Pigment was partially or wholly retracted (partially extended in two specimens; fully retracted in four specimens).

(4*b*) Darkness 1 h. Pigment was retracted (indices 1 or 2).

(4*c*) Darkness 2 h. Pigment was retracted (index 1).

Light-adapted eyes. The pigment expanded in the light (Pl. II, fig. 1).

(5*a*) Light $\frac{1}{2}$ h. Dorsally and centrally the pigment was partially extended but thin (indices 2, 3, 4). Ventrally it was extended (indices, 4, 5) and thin to dense.

(5*b*, *c*) Light 1, 2 h. The pigment was extended to a lesser extent dorsally and centrally than ventrally. Mean dorsal index 3·1; mean central index 3·8. The pigment tended to be thin, especially dorsally. Ventrally the pigment was extended (indices 4–5) and usually dense.

Cones

Dark-adapted eyes. Cones tended to elongate in darkness (Pl. I, figs. 1, 2).

(1, 2, 3) Darkness 17, 19, 31 h. In the dorsal and central fundus cones were usually fully extended (7 fish), or a fraction were extended and a fraction contracted (2 fish). In the ventral field cones were fully extended in 4 fish; part extended, part retracted (1 fish); retracted in 4 fish.

(4*a*, *b*, *c*) Darkness $\frac{1}{2}$, 1, 2 h. Cones were extended in 7 fish; part extended, part retracted in 1 fish (2 h); retracted in 1 fish (1 h).

Light-adapted eyes. The cones were usually retracted in the light (Pl. II, figs. 1, 2).

(5*a*) Light ½ h. Cones were partially or fully retracted. In the central and ventral retinae of two specimens some cones were retracted, others extended.

(5*b*) Light 1 h. Cones were mostly retracted. In the ventral retina of one specimen some cones were extended, others retracted.

(5*c*) Light 2 h. Cones were retracted.

Rods

Rods appeared to be static, but the preparations were not really suitable for following their movements, if any.

CONCLUSIONS

In the common sole the retinal pigment moves towards the external limiting membrane in the light, and towards the chorioid in the dark. Usually cones shorten in the light and elongate in darkness, but there are many exceptions, movement in the expected direction often being partial or wanting. In the light-adapted eye the pigment extends along the processes of the pigment cells and screens the outer segments of the rods (Pl. II, fig. 1). The pigment extends to the ellipsoids of the retracted cones, sometimes reaches the external limiting membrane, and comes to lie between the outer segments of the cones which are screened, to some extent from one another. Movements of pigment and cones occur in ½–1 h.

No consistent difference was noted in pigment and cones of fish killed at 12.00 h and fish killed at 24.00 h, both groups being dark-adapted. The reverse experiment, of keeping fish in light by day and night, was not tried.

In dark-adapted eyes the pigment is sometimes slightly expanded in the ventral retina when it is fully retracted in the dorsal retina. Conversely, in light-adapted eyes, the pigment is sometimes denser and extended to a greater degree in the ventral retina compared with the dorsal retina. Also movement of cones tends to be retarded to a greater degree in the ventral retina. These differences may be connected with polarity in the eye (cf. Vilter & Thibault, 1948).

SUMMARY

In the common sole *Solea solea* retinomotor changes take place. The retinal pigment usually expands in the light and cones shorten; reverse changes take place in darkness.

REFERENCES

BAYLISS, L. E., LYTHGOE, R. J. & TANSLEY, K., 1936. Some new forms of visual purple found in sea fishes with a note on the visual cells of origin. *Proc. roy. Soc.* B, Vol. 120, pp. 95–113.

GARTEN, S., 1907. Die Veränderungen der Netzhaut durch Licht. In *Handbuch der gesamten Augenheilkunde* (Graefe, Saemisch), 2 Aufl. (1925), Bd. 3, 250 pp. Berlin: Springer.

PARKER, G. H., 1932. The movements of the retinal pigment. *Ergbn. Biol.*, Bd. 9, pp. 239–91.

VILTER, V. & THIBAULT, C., 1948. Étude de méchanisme photoadaptatif du pigment rétinien melanique chez la Carpe par les éclairements unilatéraux. *C.R. Soc. Biol., Paris*, T. 142, pp. 290–2.

WALLS, G. L., 1942. *The Vertebrate Eye and its Adaptive Radiation.* 785 pp. Bull. No. 19, Cranbrook Inst. Sci., Bloomfield Hills, Michigan.

EXPLANATION OF PLATES I AND II

Sections through central retinae of *Solea solea* (magnification × 472. *e*, external limiting membrane; *c*, cones; *n.*, outer nuclear layer; *p*, pigment; *r*, rods).

PLATE I

Dark-adapted fish (2 h, 14.30–16.30 h)

Fig. 1. Pigment retracted, cones extended.

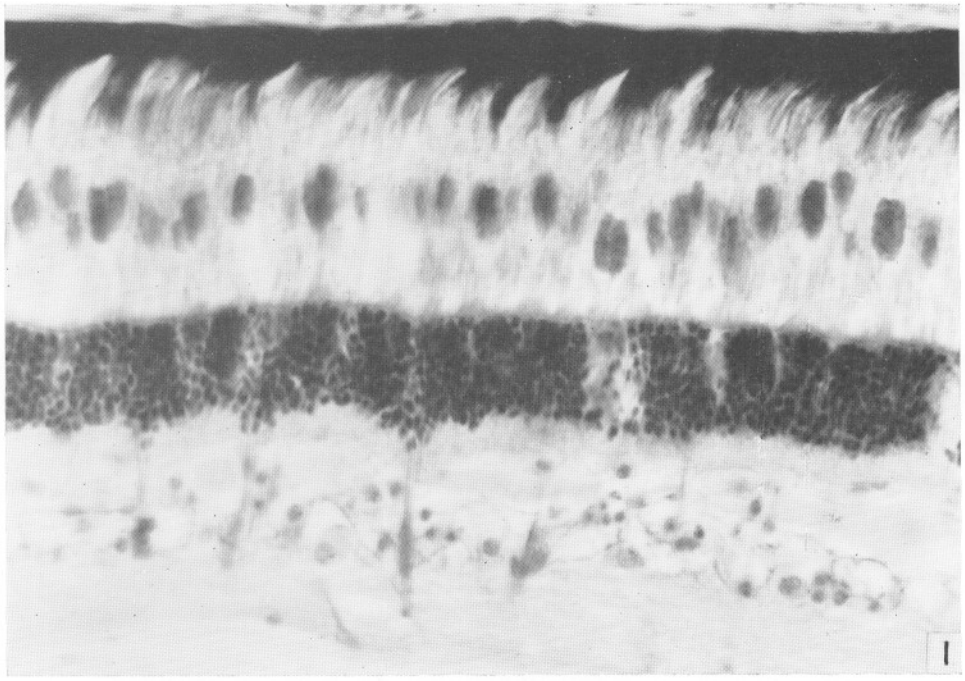
Fig. 2. Same, bleached, cones extended.

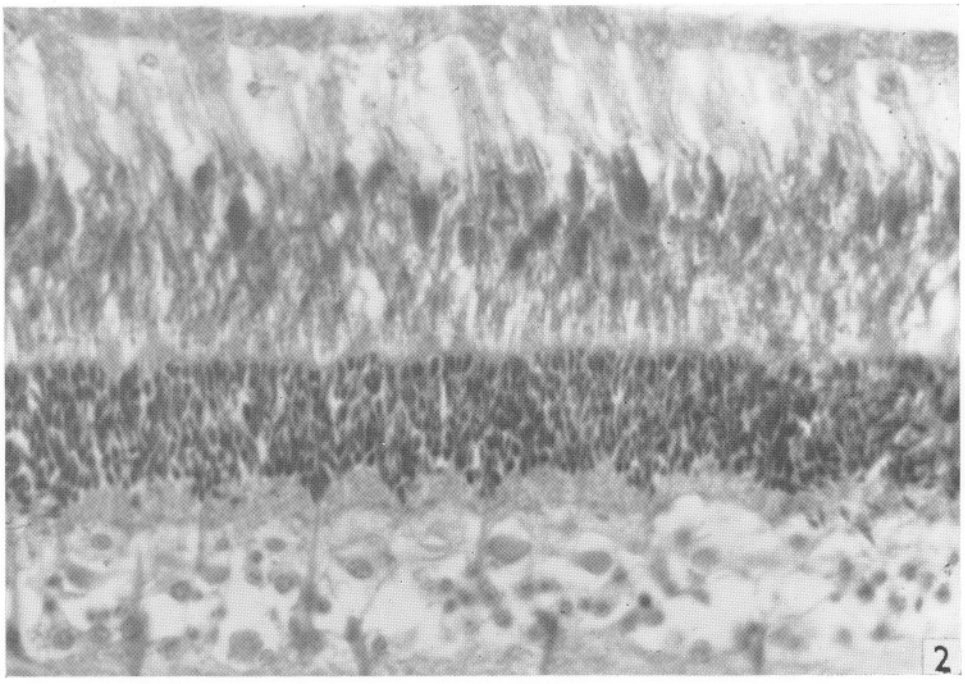
PLATE II

Light-adapted fish (2 h, 09.30–11.30 h)

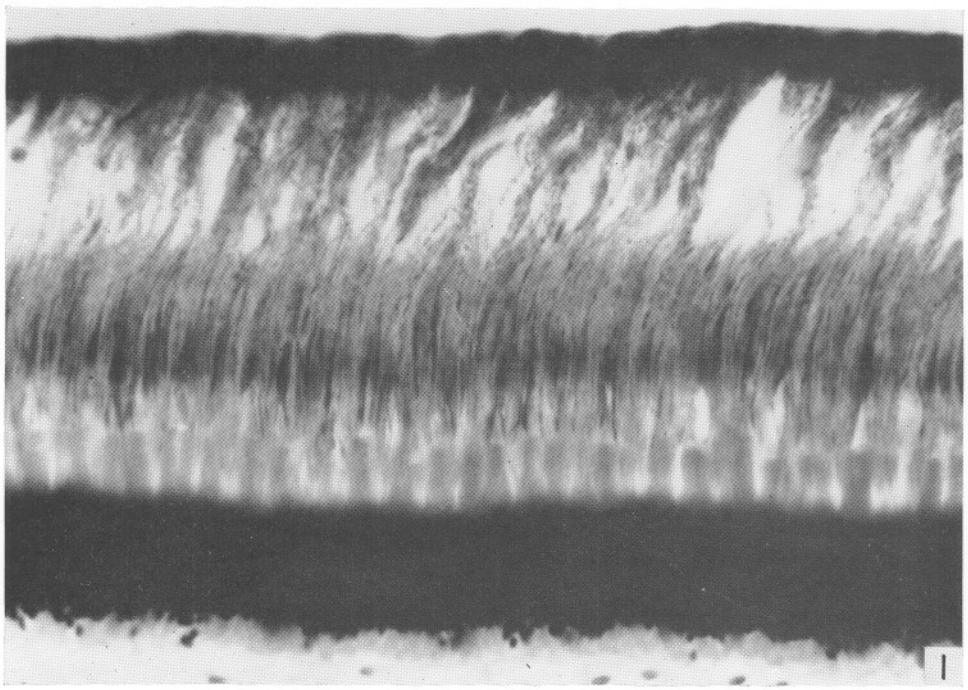
Fig. 1. Pigment extended, cones retracted.

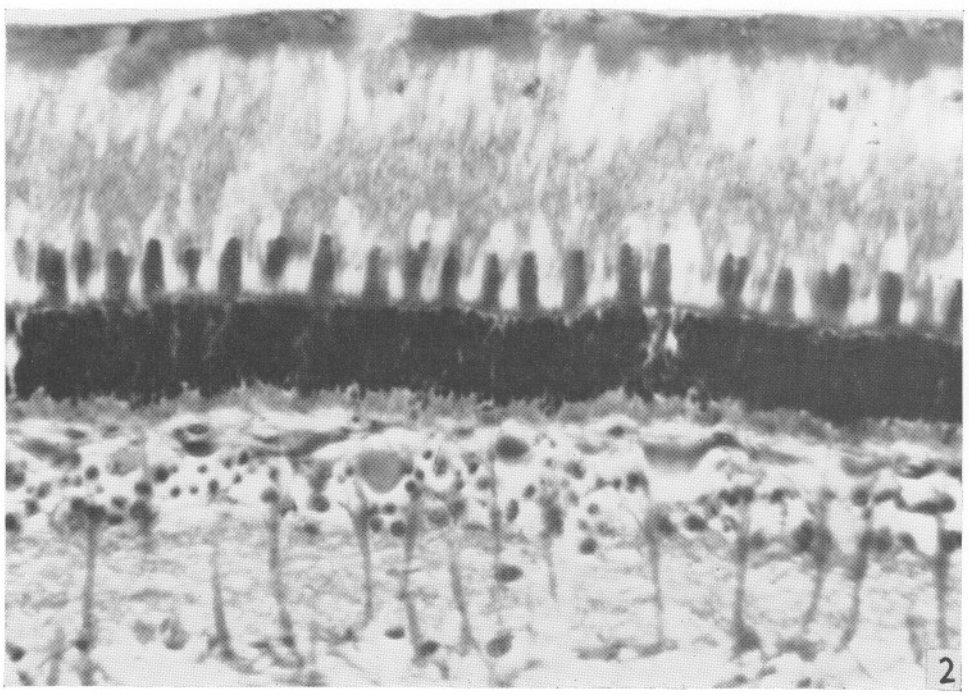
Fig. 2. Same, bleached, cones retracted.





(*Facing p.* 698)


p
c
n
1


r
c
e
n
2