

PHOTOTAXIS IN *LIMULUS* UNDER NATURAL CONDITIONS: EVIDENCE FOR RECEPTION OF NEAR-ULTRAVIOLET LIGHT IN THE MEDIAN DORSAL OCELLUS

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INTRODUCTION

A great deal of our present knowledge of basic physiological mechanisms in vision has been obtained by studying the electrical responses from the lateral eyes and the dorsal ocelli in *Limulus polyphemus* (Ratliff, 1965; Wolbarsht & Yeandle, 1967; Chapman & Lall, 1967; Lall, 1970; Nolte & Brown, 1970). Little is known about visually guided behaviour of this animal or the role of the lateral and median eyes.

Thus far laboratory investigations of visually guided behaviour in *Limulus* have yielded ambiguous results. Newly hatched *Limulus* larvae were positively phototactic (Loeb, 1893; Northrop & Loeb, 1923). Freshly collected positively phototactic young animals became negatively phototactic in less than 24 h in laboratory conditions (Cole, 1923, 1924). In a choice of two flickering light fields, young *Limulus* were attracted to the faster flickering lights (Wolf & Zerrahn-Wolf, 1937). Young animals maintained in the laboratory showed a weak optokinetic response when the animals entered a T-maze illuminated by a rotating pattern of vertical stripes (von Campenhausen, 1967). Besides these observations, illumination of the lateral eye caused leg movement of the contralateral side and also modified ongoing cardiac rhythm (Corning & von Burg, 1967).

Classical (Smith & Baker, 1960; Makous, 1969) and operant conditioning (Makous, 1969) techniques have yielded marginal results. Some conditioning occurred in both cases, but 'a useful technique has yet to be developed' (Makous, 1969). Subsequent to a report of avoidance conditioning in *Limulus* (Wasserman & Patton, 1969) control conditions indicated that downward tail movement was an unconditional response to sudden light onset in some naïve animals (Wasserman & Patton, 1970). This response was stable enough in some animals to enable the first absolute threshold to be obtained by means of the staircase method.

None of the studies discussed above separated stimulation of the lateral eyes from stimulation of the median eyes. This point and the irregularity of the response in laboratory experiments led the present authors to study visual orientation of *Limulus* in its natural habitat under natural sunlight, separately stimulating lateral and

median eyes. In this study phototaxis is used as an index of visual behaviour. The question whether either lateral eye alone or median eye alone can mediate positive phototaxis was investigated. Since electrophysiological study has shown that *Limulus* median eye possesses two spectral mechanisms, u.v. and visible (Wald & Krainin, 1963; Lall & Chapman, 1964; Chapman & Lall, 1967; Lall, 1970; Nolte & Brown, 1970), the further question of whether both mechanisms can mediate phototaxis was also investigated. Evidence is presented here to show that visual orientation to u.v. light is mediated by the ocellus.

MATERIAL AND METHODS

Animals and location

Experiments were conducted on a gently sloping, quiet, undisturbed estuarine beach located on an island off the coast of New Jersey, called the 'Little Beach', part of Brigantine National Wildlife Refuge. *Limulus* came to this beach for mating and egg-laying during the months of May and June. The experimental animals were mature (♂ and ♀) *Limulus*. Some of the animals were collected as they were swimming in the shallow water of the lagoon, others while they were either crawling around on the beach or stranded on the moist area of the beach where they had come during the high tide but were left behind as the tide receded. These experiments were conducted between 10.30 and 19.00 h, and the air temperature ranged from 20 to 24 °C. The sky was bright and hazy.

Preparation

Immediately after an animal was picked up, it was washed and its eyes were cleaned for experimentation. The eyes to be occluded were covered with black electrical tape. Through one layer of such tape the sun was not visible to a human observer after 20 min of dark adaptation. As a control for pressure, transparent cellophane tape was put on the naked (i.e. unoccluded) eye in some experiments. For restricted-spectrum experiments Corning glass filters were mounted on the naked eye with black electrical tape.

General procedure

Three of the four photoreceptors (two lateral eyes and two dorsal ocelli) were occluded and one eye was left naked. The question was whether the behaviour of the animal was influenced by the eye receiving the light. The subject was then released on the beach above the water line. The tracks of its movements were transcribed on to a sheet of paper and updated periodically (Fig. 1). As many as 16 animals were simultaneously observed on the beach. After each subject had been observed for some time, the occlusion was shifted to the opposite side to control for turning bias. For example, if the left lateral eye was naked in the initial condition, then the right lateral eye was naked on the reversed condition, the remaining eyes being occluded. In each experiment the animals were about evenly divided with respect to whether the right or the left eye was naked in the initial condition.

Uni-ocular photic stimulation tended to produce turns in the direction of the naked eye (Fig. 1). This tendency was quantified by counting the number of left and right turns, where a turn was arbitrarily defined as a 90° change in the direction of the track.

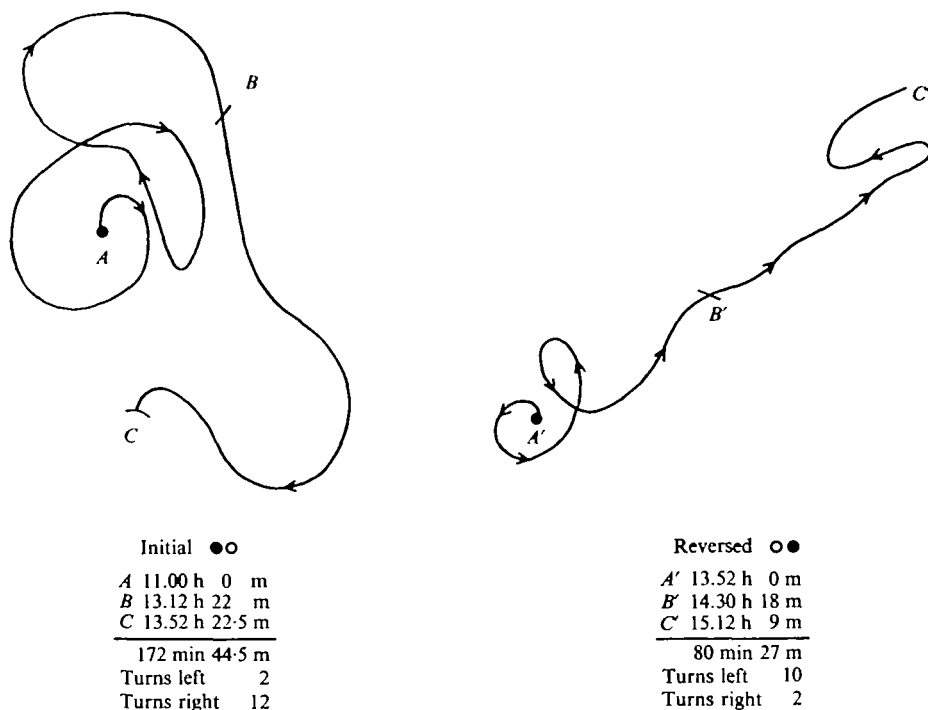


Fig. 1. Transcribed tracks for one *Limulus* (no. 56). Two lateral eyes and one ocellus occluded. U.v. filter (Corning Cs7-60) mounted on the naked ocellus. Right ocellus was naked in the initial condition while the left ocellus was naked in the reversed condition.

This measure does not necessarily reflect discrete, temporally organized turns of the *Limulus*, but rather digitizes the continuous track into arbitrary units. Total linear distance of the track and duration of each session were also tabulated.

Experimental design

Experiment I. The first experiment dealt with the lateral eyes under full-spectrum sunlight. In this experiment both ocelli were always occluded.

Experiment II. The second experiment dealt with the dorsal ocelli stimulated by full-spectrum sunlight with the lateral eyes always occluded.

Experiment III. In the third experiment the dorsal ocelli were stimulated by restricted regions of the solar spectrum (Fig. 2). Corning filters passing either the near-u.v. (Cs7-60, maximum transmission 360 nm) or the visible region of the spectrum (Cs3-69, 50% transmission above 530 nm) were mounted on the naked ocellus with black electrical tape. Three groups of animals were used. For the u.v. group filter Cs7-60 alone was used. For the visible-wavelength group only Cs3-69 was used. In the third group as a control condition both filters were mounted together on the naked ocellus, thus excluding light radiation except far red from the ocellus.

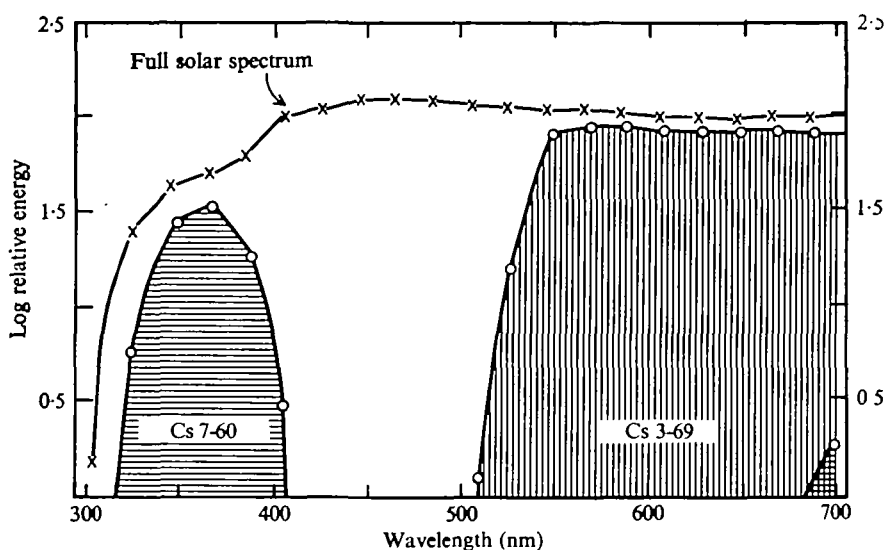


Fig. 2. Spectral distribution of solar radiance (after Hennes & Dunkelman, 1967 (300–400 nm), and Smith & Tyler, 1967 (400–700 nm)). The solar radiation passing through filters Cs 7–60 (horizontal lines) and Cs 3–69 (vertical lines) are also plotted.

Spectral distribution of solar radiance

Recent studies by Hennes & Dunkelman (1967) (300–400 nm) and Smith & Tyler (1967) (400–700 nm) have been used to obtain the relative energy of the sunlight (Fig. 2). When Corning filters were used, a quantitative estimate of the total stimulative energy in each region (u.v. and visible) could be obtained as follows. If at each wavelength the log relative transmittance for the Corning filters was added to the log relative energy of the solar spectrum, then the two curves obtained would represent the log relative energy in the u.v. and the visible region of the spectrum reaching the eye. Integrating the area under these curves would give the total energy in each region. A simplified technique used here was to add the values under the curves in the two regions at 20 nm steps from 320 to 700 nm. The effective energy impinging on the ocellus in the u.v. regions of the sunlight was 1/10 of the energy present in the visible region.

Scoring methods

In order to quantify the phototactic activity, various measures were taken. The first set of measures indicating each group's phototactic activity were: (a) the percentage of turns made towards the naked eye (Table 1, col. V) out of the total number of turns made by each group, and (b) net turns towards the naked eye per animal (Table 1, col. VI), obtained by subtracting the number of turns towards the occluded eye from the number of turns towards the naked eye and then dividing by the number of individuals in each group. The phototactic effects were statistically assessed in each group by Wilcoxon matched-pair signed-rank tests ($\alpha = 0.01$) based on the net turns towards the naked eye for each animal.

Besides these group analyses it was also necessary to consider whether each animal was positively or negatively phototactic. If the score (net turns towards the naked eye)

Table 1. Summary of phototactic behaviour in *Limulus* with only one eye naked, and the others occluded, either lateral or median, under full-spectrum and restricted-spectrum sunlight conditions, amount of turning, length of track and duration of trial

No.	Eye stimulated (I)	Light at eye (II)	No. of animals (III)	No. of turns towards eye		Turns towards naked eye (%) (V)	Mean net turns* (VI)	% of animals positively phototactic at $\alpha = 0.025$ (VII)	Time (min) (VIII)	Distance (metres) (IX)	Crawl rate (m/h) (X)	Turn rate (turns/h) (XI)
				Naked	Occluded (IV)							
1	1 lateral eye	Sun	8	111	17	87	+11.7	50	97	23	14.0	4.8
2	1 ocellus	Sun	33	560	297	65	+8.0	33	91	23	15.5	8.8
3	1 ocellus	U.v.	12	308	119	72	+15.7	33	99	23	13.5	10.7
4	1 ocellus	Visible	11	192	177	52	+1.4	0	96	22	16.5	10.6
		> 520 nm										
5	1 ocellus	Far red	11	171	157	52	+1.3	0	84	24	16.7	10.5
		> 680 nm										

* Measure taken per animal.

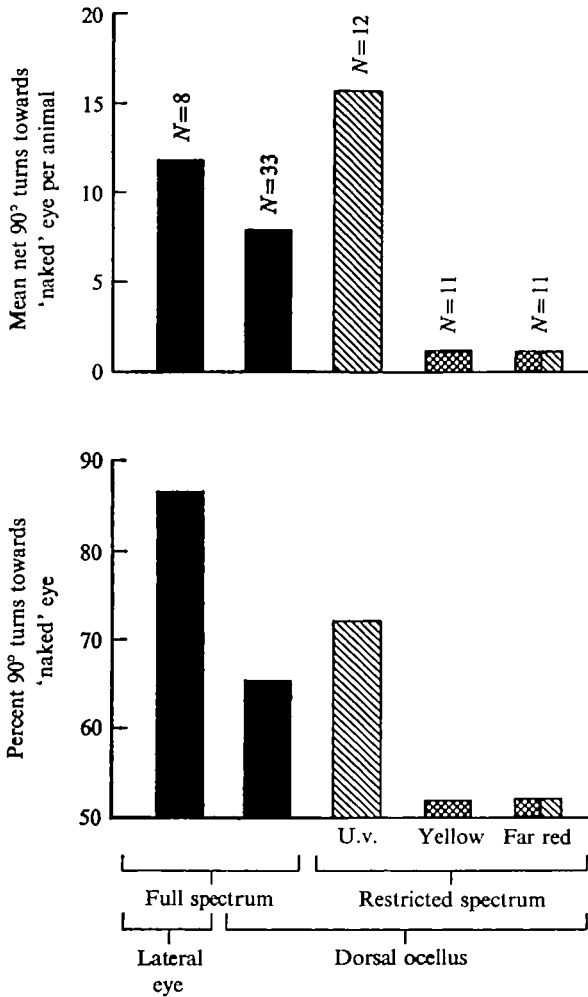


Fig. 3. Percent and mean net 90° turns towards the naked eye for lateral eye and dorsal ocellus in *Limulus* under full-spectrum and restricted-spectrum sunlight.

was positive the animal could be considered positively phototactic. Most of the individuals in groups 1, 2 and 3 met this criterion. In addition, a more stringent criterion was used by ascertaining whether this positive score was statistically significant. For each *Limulus* the proportion of turns towards the naked eye was tested against a chance hypothesis of 0.5 by a binomial distribution test (one tail, $\alpha = 0.025$). The percentages of individuals reaching this criterion are shown in Table 1, col. VII.

RESULTS

For clarity the group analyses are presented first, after which the results of the individual analyses are summarized.

Lateral eye phototaxis under full-spectrum sunlight. The turns towards the naked eye exceed those towards the occluded eye for all animals; the mean net turns per animal was +11.7 (Fig. 3). The hypothesis that the difference between the turns

towards the naked and those towards the occluded eye is attributable to chance was rejected at $\alpha = 0.01$ (Wilcoxon matched-pair signed-rank test, $N = 8$). Eighty-seven % of the turns were towards the naked eye (Table 1, col. V). The durations for various trials lasted from 60 to 154 min, during which the animals covered distances ranging from 3 to 60 m. The distance did not affect the tendency to turn towards the naked eye. The activity level of the animals in the initial and the reversed conditions was about the same as evidenced by mean crawl rates of 12 and 16 m/h and mean turns per hour of 4.2 and 5.4, respectively.

Dorsal ocelli phototaxis under full-spectrum sunlight. The net turns towards the naked ocellus were positive for 75 % of the animals, the mean net turns per animal being +8.0 (Fig. 3). The hypothesis that the difference between the turns towards the naked eye and those toward the occluded eye is attributable to chance was rejected at $\alpha = 0.01$ (Wilcoxon matched-pair signed-rank test, $N = 33$). For this group 65 % of the turns were towards the naked eye. The duration of the trials varied from 40 to 157 m. In the initial and reversed conditions the animals travelled at average rates of 17.6 and 13.3 m/h making 10.5 and 7.1 turns/h respectively.

Dorsal ocelli phototaxis under restricted-spectrum sunlight. In one group of 12 animals the ocelli were stimulated by u.v. light of the sun (Fig. 2). The net turns towards the naked ocellus were positive for 91 % of the animals, the mean net turns per animal being +15.7 (Fig. 3). The hypothesis that the difference between the turns towards the naked eye and those towards the occluded eye is attributable to chance was rejected at $\alpha = 0.01$ (Wilcoxon matched-pair signed-rank test, $N = 12$). The trial durations were 20–197 min. In the initial and reversed conditions the animals travelled at average rates of 15.5 and 11.6 m/h making 11.8 and 9.6 turns/h respectively.

On a second group of 11 animals, yellow cut-off filters were used which allowed only the medium-to-long wavelength part of the visible spectrum to stimulate the naked ocellus (Fig. 2). Of the 11 animals 6 made more turns towards the naked ocellus and 5 toward the occluded ocellus; 52 % of the turns were towards the 'naked' ocellus, the mean net turns per animal being +1.4 (Table 1, Fig. 3). The two-tailed probability of obtaining differences as large as these by chance is approximately 0.6 (Wilcoxon matched-pair signed-rank test, $N = 11$). Thus it appears that visible light had no reliable effect on the ocelli. The duration of the trials was 38–195 min. In the initial and reversed conditions the animals travelled at average rates of 16.3 and 16.7 m/h making 13 and 8 turns/h, respectively.

The fifth group was the 'far red' group of 11 animals, where both yellow and u.v. filters were mounted on the naked eye so as to allow through only far-red radiation. Four animals were positively phototactic, five negatively and two scored zero. Only 52 % of the turns were towards the naked ocellus and the mean net turns per animal was only +1.3. The two-tailed probability of obtaining differences at least as large as these by chance is approximately 0.6 (Wilcoxon matched-pair signed-rank test, $N = 11$). These chance-performance data demonstrate the lack of bias in the technique and consequently constitute an important control. The durations of the trials were 22–85 min. In the initial and reversed conditions the animals travelled at average rates of 19 and 14.6 m/h, making 12.5 and 8.5 turns/h respectively.

The results of the five experiments are summarized in Fig. 3, where the percentage of 90° turns as well as mean net turns towards the naked eye are plotted. A larger

phototactic effect was obtained with the lateral eye than with the dorsal ocellus, when stimulated by full-spectrum sunlight. Comparing the dorsal ocellus data under three conditions, it appears that the u.v. part of the solar spectrum has a marked phototactic effect whereas the visible portion does not. It should be pointed out that other measures, i.e. time, distance and crawl rate, were comparable in the five experimental conditions. When the lateral eye alone was stimulated, turn rate tended to be about half of that when the ocellus alone was stimulated.

Besides the lateral eyes and dorsal ocelli, *Limulus* also has a ventral eye. But this eye would not affect our results as the eye is shaded by the animal on the ventral side and is located on the midline.

Individual statistics. In addition to the group statistics described above, the data were also analysed for each animal separately in order to provide a fuller description of the data. For each animal the proportion of turns toward the naked eye was tested against a chance hypothesis of 0.5 by a binomial distribution test (one tail, $\alpha = 0.025$). The percentages of individuals reaching this criterion are shown in Table 1, col. VII. None of the individuals met this criterion in groups 4 and 5, where the naked ocellus was stimulated only with long-wavelength visible light or far-red light. In contrast to these 0% base-lines, groups 1-3, which received full-spectrum stimulation of lateral eye and ocellus and u.v. stimulation of ocellus had 55, 33, and 33% of their individuals reaching this stringent criterion. Thus, the analyses of the individual data support the same conclusions obtained with the group analyses.

The effects could be statistically significant for the group and not for individuals within the group for two reasons: (a) some of the individuals within the group may be different from the rest and/or (b) the data obtained may not have sufficient observations to overcome the technical statistical hurdles of the variance and degrees of freedom. Although we cannot distinguish between these two possibilities with certainty, the second reason appears to be more applicable to these data.

DISCUSSION

Phototaxis and the lateral eye. Among the arthropods compound lateral eyes are used for visual orientation (Fraenkel & Gunn, 1961; Dufay, 1964; Cassier, 1965). Laboratory experiments in photo-orientation, where distinctions between stimulating the lateral eyes and dorsal ocelli were not made, have described *Limulus* to be positively phototactic (Loeb, 1893; Cole, 1923, 1924; Wolf & Zerrahn-Wolf, 1937; von Campenhausen, 1967) and negatively phototactic (Loeb, 1893; Northrop & Loeb, 1923; Cole, 1924).

Our experiments in the field utilizing occlusion techniques showed that lateral eyes were sufficient in mediating positive phototaxis (Table 1) in fresh mature *Limulus*, in the absence of ocellar input. This agrees with the findings among the Insecta, where a great deal of work on photo-orientation (Dufay, 1964; Cassier, 1965; Jander & Barry, 1968) indicates that the lateral compound eyes mediate positive phototaxis.

Phototaxis and the dorsal ocellus. The positive phototaxis mediated by dorsal ocelli in *Limulus* is not an isolated phenomenon among the invertebrates. The dorsal ocelli in the sawfly, *Sarcophaga aldrichi* (Wellington, 1953), and in the nocturnal lepidopterans

Noctua pronuba and *N. fimbriata* (Dufay, 1964), are known to mediate phototaxis. Our data indicated that the dorsal ocelli mediate positive phototaxis under near-u.v. stimulation but not under visible light stimulation. Furthermore, the strength of the response was greater under u.v. stimulation than under full-spectrum light, which contains both u.v. and visible wavelengths (Table 1 and Fig. 3). Is it not probable, as Dufay (1964) has suggested, that the visible wavelengths have an inhibitory effect on positive phototaxis?

Behavioural evidence shows that the honeybee, *Apis*, distinguishes u.v. as a specific hue (Daumer, 1956). The data presented above do not show whether *Limulus* responds preferentially to near-u.v. on the basis of either brightness or hue. It was estimated that the stimulatory energy of the solar spectrum passing through the u.v. filter was one-tenth that passing through our visible filter (Fig. 2). If the high relative spectral sensitivity of the ocellus to the u.v. wavelengths (dark-adapted sensitivity curve, fig. 11, Chapman & Lall, 1967) is taken into account, then the effective energy absorbed by the ocellus is 75 times more in the u.v. than in the visible region. The estimates of the effective energy absorbed by the ocellus were made by adding the log relative energy of the restricted solar spectrum transmitted by Corning filters (Fig. 2) and the log relative spectral sensitivity of the dark-adapted ocellus obtained by electrical recording at 20 nm intervals.

The energy estimates for the u.v. part of the solar spectrum (Fig. 2) obtained by Hennes & Dunkelman (1967) were obtained at high altitudes (8025 ft). These measures might not be strictly comparable to the u.v. radiance at sea level, Brigantine, New Jersey. Similarly, the energy estimates for visible wavelengths might not be comparable between Brigantine and Crater Lake, Oregon (elevation, 6239 ft), where Smith & Tyler (1967) made their spectral measurements.

Our study showed that both lateral eyes and dorsal ocelli in *Limulus* are effective in visual orientation. But the question as to what specific roles the eyes play in the whole behavioural repertoire of the animal is still unanswered. One often observes in the field mature *Limulus* that are blinded owing to injury or the growth of marine plants and ectocommensals on the eyes. Such blind animals have been seen swimming and mating. It appears that they can survive without a proper functioning of their photoreceptors, but this fact does not prove that they survive as well on the average as do animals with normal vision.

The function of the ocellus and its possible role in Limulus. The function of the ocellus in the invertebrates is problematic. A variety of functions has been ascribed to it: (a) photokinesis, (b) orientation, (c) potentiation of phototactic response, (d) perception and monitoring of luminosity in the environment, and (e) neuroendocrine function.

Wolsky (1930) suggested that the ocellus in invertebrates is a 'stimulatory organ'. The photokinetic reactions in *Planaria* (Walter, 1907) and in marine turbellarians (Mast, 1923) are mediated through their ocelli. When compound eyes are also present besides the ocelli, the ocelli function in co-operation with the compound eyes as photokinetic organs. This hypothesis is confirmed particularly on *Drosophila melanogaster* (Médioni, 1959), on *Locusta migratoria migratorioides* (Parry, 1947; Cornwell, 1955; Cassier, 1962, 1965; Jander & Barry, 1968), on *Blattella germanica* (Goustard, 1958) and on the cricket, *Gryllus bimaculatus* (Jander & Barry, 1968).

If accord seems to have been reached on this point, much more controversy exists regarding the role of the ocellus in photic orientation. Though orientation is a function of the compound eye, the ocellus is also given some credit for it (Cornwell, 1955; Goustard, 1956; Médioni, 1959; Cassier, 1962; Dufay, 1964). The ocelli appear to control the strength of the phototactic activity in *Locusta migratoria* and *Gryllus bimaculatus*, having a synergistic action with the compound eye under weak illumination and an antagonistic action under strong illumination (Jander & Barry, 1968). In all these studies the role of the ocellus is either to potentiate or inhibit the response elicited by the compound eye.

The fourth function of the ocellus is believed to be the indication of luminosity and its rapid variations (Parry, 1947; Hoyle, 1955; Autrum & Metschl, 1961). This function cannot be separated completely from the functions discussed earlier. Unioocular occlusion causes increases in the latency of the phototactic reactions in *Drosophila melanogaster* (Médioni, 1959) and in *Locusta migratoria migratorioides* (Cassier, 1962, 1965). The luminosity-monitoring properties may be inferred from the ocellar size. The nocturnal bees (*Hymenoptera*, *Apoidea*) have larger ocelli than those that forage only in daylight (Kerfoot, 1967). Similarly, nocturnal butterflies (*Noctuidae*) have larger ocelli than diurnal species (Dufay, 1964).

The output of the ocelli is reported to influence the circadian rhythm in the cockroach (Harker, 1956). As light is registered by the ocelli, messages are sent to the suboesophageal ganglion which is neurosecretory in function and regulates the biological clock. The ocellar output in flesh flies, as well as in the cockroach, is also reported to regulate brain excitability (Mimura *et al.* 1969).

Our studies on the *Limulus* median ocellus (Fig. 3) show that a u.v.-light stimulus elicits a positive phototactic response. This response may be correlated with the spike potential elicited by illumination in the ocellar nerve (Waterman, 1953) and is restricted to u.v. light (J. Nolte & J. Brown, personal communication). A thorough investigation of this problem is needed before any conclusions can be drawn. The significance of a u.v.-light receptor in the *Limulus* median ocellus and its specific function in the life-cycle is problematic. The vertical movements in Cladocera are governed by ocelli in the presence of u.v. light (Baylor & Smith, 1957). The same may be true for *Limulus*. We have obtained a threshold ERG from an ocellus at very low levels of illumination ($1.4 \times 10^{-10} \mu\text{W}/\text{cm}^2/\text{nm}$ at 360 nm). Recent studies provide a figure of $10^{-3} \mu\text{W}/\text{cm}^2/\text{nm}$ at 533 nm (Kampa, 1970) and $2 \times 10^{-4} \mu\text{W}/\text{cm}^2/\text{nm}$ at 360 nm (Biberman & Nudelman, 1971) for moonlight. The last value is about 1 000 000 times brighter than the low-level test flash in ERG experiments. From these calculations it can be inferred that *Limulus* median ocellus can respond to moonlight illumination on the beach at 360 nm. The turbid coastal waters at the depth of 20 m would attenuate the light by a factor of approximately 1/10 000 (Clarke & Denton, 1962). Thus moonlight at 360 nm reaching 20 m depth would be about $2 \times 10^{-8} \mu\text{W}/\text{cm}^2/\text{nm}$, which is still about 143 times brighter than the low-level test flash in the ERG experiments. From these calculations it can be hypothesized that there exists a likelihood of *Limulus* median ocellus detecting near-u.v. light of the moon at a depth of 20 m. Thus the median ocellus in horseshoe crabs could be used as a depth detector to guide the animals to shallow waters and to the beach for reproductive functions.

SUMMARY

1. Phototactic behaviour in *Limulus* mediated by lateral eye and dorsal ocellus was studied under full-spectrum and restricted-spectrum (near-u.v. and visible light) sunlight on a beach.
2. All eyes (lateral eyes, dorsal ocelli) were occluded excepting one, which mediated the response.
3. It was found that either a lateral eye or a dorsal ocellus alone could mediate positive phototaxis in adult *Limulus* under full-spectrum sunlight.
4. When the sunlight stimulating the dorsal ocellus was filtered into restricted wavelengths, the near-u.v., but not the visible light, elicited positive phototaxis.

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