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RETINAL ORIENTATION AND THE DISCRIMINATION OF POLARIZED LIGHT BY OCTOPUSES

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INTRODUCTION

Moody & Parriss (1961) showed that *Octopus* was capable of discriminating between two sources of plane polarized light, whose planes of polarization were at right angles. These experiments did not entirely eliminate the possibility of a discrimination based on differential reflexion. The experiments described below confirm that *Octopus* can distinguish between sources emitting light polarized in different planes and show that discrimination is maintained under conditions in which reflexions from the walls or contents of the aquaria or from the water surface are made to vary unsystematically.

METHOD

The slit pupil of the eye of *Octopus* normally remains horizontal, indicating that the retina remains constantly oriented with respect to gravity, whatever the position of the rest of the animal. Wells (1960) showed that if both statocysts are removed this regular orientation is lost. After the operation pre-trained animals continued to discriminate between black and white objects but were unable to distinguish between rectangles differing only in orientation. If, however, the rectangles were shown with the axes formerly parallel to the horizontal now parallel to the pupil, the discrimination continued.

If *Octopus* was basing its discrimination of polarized light sources on internal reflexions, then discrimination would only continue as long as the plane of polarization was oriented in a particular way to the fixed reflecting surfaces. By removing the statocysts and matching the electric vector to the (now irregular) orientation of the pupil, the plane of polarization is made to take up a random series of orientations with respect to the fixed reflecting surfaces. If discrimination continues under these conditions, it can be concluded that the discrimination is *not* based on differential internal reflexion.

MATERIALS AND TRAINING PROCEDURE

Small *Octopus vulgaris* Lamarck, weighing between 15 and 30 g., were obtained from the Bay of Naples and tested during July and August 1961. They were kept singly in wooden aquaria measuring 40 × 20 × 15 cm., set up as described by Wells (1960).

A torch emitting plane polarized light was constructed in the following manner. A 6 V. torch bulb was embedded in paraffin wax in a glass tube 4 cm. long and 1·5 cm. in diameter. Leads to the bulb passed out through a rubber bung in the rear end of the tube. In front of this light source were arranged a further 1 cm. of paraffin wax, and a disk of Polaroid plastic, 1·5 cm. diameter. The whole assembly was placed inside a clear glass specimen tube 5·2 cm. long and 1·75 cm. outside diameter. The inside of this tube was lined with opaque black paper. The resultant torch is shown in Fig. 1. In front view it presents a 1·5 cm. disk of illuminated polaroid, surrounded by a 1 mm. ring of non-polarized light, transmitted through the glass walls of the specimen tube. The torch was held on the end of a probe by concentric rings of wire round the outer tube. This type of construction has the following advantages:

(*a*) Its total size is small relative to the area of polaroid it presents.

(*b*) The polaroid disk is loose relative to both the wax and the overlying glass, so that slight irregularities in these two surfaces are altered unsystematically in successive presentations. This avoids a false discrimination based upon these cues.

There are no external markings indicating the vector position. This was set before each test by examining the torch through another piece of polaroid. At intervals throughout the testing period the polaroid and the diffusing wax were replaced by new material.

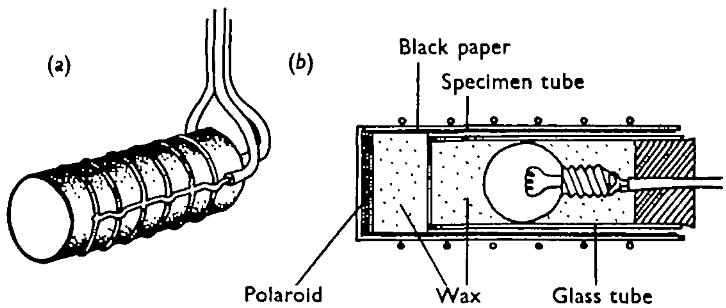

Fig. 1. The torch used in the experiments. (*a*) Shows the wires through which shocks were given and (*b*) is a section, showing internal construction. The external specimen tube, with the Polaroid sheet held in place by a wax plug, could be rotated around the internal tube containing the light source.

During training, the torch was placed in the aquarium as far as possible from the octopus, and was moved slowly up and down and from side to side for 30 sec., or until the octopus attacked it. Throughout the series the positive object was the torch with the electric vector normal to the pupil, and the negative object was the torch with the electric vector parallel to the pupil. Attacks on positive objects were rewarded with a piece of prawn, attacks on negative objects punished by a 6 V. a.c. shock given through the wire rings around the torch.

After removal of the statocysts, some modifications were necessary. Since the orientation of the retina is liable to alter as soon as the animal moves its head, the torch was presented near enough for the octopus to reach out and touch it with one arm (see Wells, 1960). Further, some of the animals had learned by this time to avoid the wire rings when touching the torch, and the punishing shock was therefore administered through a probe.

Before testing began the animals were pre-trained for 2 days, at eight trials per day, on the positive object only, and all reached 100% attack level on the second day. During testing, the positive and negative objects were each presented four times a day in the following sequence. First day: + − + − + + − −; second day: − + − + − + + −, and so on.

RESULTS

Ten animals were trained; one of these escaped and died on day 8. The other individuals made from 16 to 35 attacks out of a possible 80 during the 10 days of pre-operational training. The complete data for these animals are given in the first part of Table 1.

Table 1. *Numbers of attacks made in the positive (electric vector normal to pupil) and negative (electric vector parallel to pupil) situations before and after removal of the statocysts*

	Animal																				
	A		C		G		H		K		L		M		O		P		Q		Total	
Day	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−
1	3	3	2	2	3	2	4	3	1	2	1	2	4	2	3	3	3	2	4	2	28	23
2	2	1	2	0	0	1	3	2	3	2	2	1	1	1	3	2	3	1	4	2	23	13
3	3	1	1	1	2	1	3	2	2	0	2	0	2	1	2	1	2	1	3	2	22	10
4	3	1	1	1	0	0	4	1	2	0	2	1	1	2	3	1	1	1	3	1	20	9
5	1	1	0	0	1	0	2	1	2	2	1	1	1	1	1	0	2	1	2	0	13	7
6	1	1	2	0	3	0	3	1	1	1	2	2	2	2	2	2	3	2	2	0	21	11
7	0	0	0	1	2	0	3	1	0	0	4	0	2	0	1	1	1	0	4	0	17	3
8	0	0	1	0	1	0	2	1	2	0	4	2	3	1	3	0	1	0	1	3	18	7
9	0	0	1	1	2	0	3	2	0	0	2	0	4	2	4	2	.		3	1	19	8
10	0	0	0	0	1	0	0	0	2	1	3	1	3	0	4	0	.		4	1	17	3
Total +	13		10		15		27		15		23		23		26		16		30		198	.
Total −		8		6		4		14		8		10		12		12		8		12	.	94
11	Operation—both statocysts removed																					
12	3	1	2	2	4	1	0	1	1	0	0	0	2	1	4	1	.		.		16	7
13	3	2	3	1	1	1	3	0	1	1	2	0	2	1	1	4	.		.		16	10
14	0	2	2	0	2	0	4	1	2	2	1	0	2	0	2	1	.		.		15	6
15	2	0	0	1	3	0	0	1	3	2	.		3	1	3	1	.		.		14	6
16	1	1	1	0	4	1	2	1	1	2	.		1	2	1	1	.		.		11	8
17	0	1	1	1	2	0	2	1	2	1	.		1	2	2	0	.		.		10	5
18	1	0	0	0	0	0	.		0	0	.		4	2	4	0	.		.		9	2
19	2	0	1	0	1	1	.		3	2	.		2	1	1	0	.		.		10	4
20	1	1	1	1	2	2	.		1	1	.		1	1	1	1	.		.		7	7
21	1	1	2	1	2	1	.		2	2	.		0	0	4	1	.		.		11	6
Total +	14		13		21		11		16		3		18		23		.		.		119	.
Total −		9		7		7		4		13		0		11		10		.		.	.	61

On day 11, eight of the nine surviving animals were anaesthetized with urethane, and the statocysts removed. The experiment with the remaining animal (Q in table 1) was begun after the others and there was no time left for post-operational training. On day 12 training was resumed, this time with the electric vector matched to the now randomly oriented pupil. During this period two animals were killed by an overnight breakdown in the seawater circulation. The remaining six were trained for 10 days. The data for all the animals are given in the second half of Table 1; individuals trained for the full 10 days made from twenty to thirty-three attacks, so that the level of response was about the same as in pre-operational training.

From Table 1 it can be seen that the total numbers of attacks on positive and negative objects respectively were 198 and 94 before operation, and 119 and 61 afterwards;

in both cases the difference is significant (two-cell table of χ^2 for equal expected frequencies, $P < 0{\cdot}01$).

Probably it would be safe to conclude from this alone that:

(*a*) The animals discriminated between the positive and negative objects, and

(*b*) That they continued to do so after statocyst removal.

But more accurate information can be obtained in the following way.

Table 2 and Fig. 2 show the average number of attacks made on the positive and on the negative object for each day of the testing period. Table 2 also shows the ratio (R) between these averages for each day. In it the average values of $\bar{R}$ (R) are calculated for the pre-operational and post-operational periods, being $2{\cdot}81 \pm 0{\cdot}55$ and $2{\cdot}25 \pm 0{\cdot}33$, respectively. As these values are significantly (0·001) above unity, it is confirmed that the animals distinguish between the positive and negative objects;

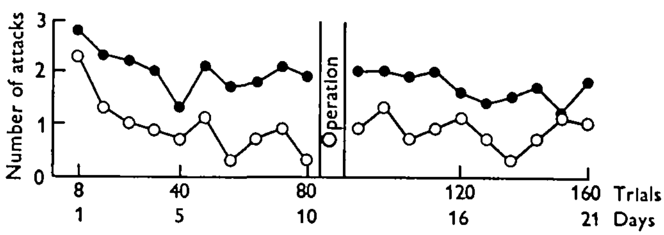

Fig. 2. The effect of statocyst removal on performance in a polarized light discrimination. ● shows the number of attacks in the +ve situation (electric vector normal to the pupil) and ○ the number of attacks in the −ve (vector parallel with the pupil) in each day of 8 trials (4+, 4−). Averages from ten animals, which had 2 days (16 trials) of pre-training to attack in the positive situation before the start of the experiment. On day 11 both statocysts were removed.

Table 2. *Average number of attacks per day in the positive and negative situations* ($\bar{x}+$ *and* $\bar{x}-$), *and the ratio* (R) *of the positive to the negative average*

Day	$\bar{x}+$ av. no. + attacks	$\bar{x}-$ av. no. − attacks	R ($\bar{x}+/\bar{x}-$)	
1	2·8	2·3	1·22	Pre-operation: $\bar{R} = 2{\cdot}81 \pm 0{\cdot}55$
2	2·3	1·3	1·77	
3	2·2	1·0	2·20	
4	2·0	0·9	2·22	
5	1·3	0·7	1·86	
6	2·1	1·1	1·91	
7	1·7	0·3	5·67	
8	1·8	0·7	2·57	
9	2·1	0·9	2·33	
10	1·9	0·3	6·33	
11		Operation		
12	2·0	0·9	2·22	Post-operation: $\bar{R} = 2{\cdot}25 \pm 0{\cdot}33$
13	2·0	1·3	1·54	
14	1·9	0·7	2·71	
15	2·0	0·9	2·22	
16	1·6	1·1	1·46	
17	1·4	0·7	2·00	
18	1·5	0·3	5·00	
19	1·7	0·7	2·43	
20	1·2	1·1	1·10	
21	1·8	1·0	1·80	

and as they do not differ significantly from each other it is confirmed that the octopuses continue to discriminate just as well after removal of the statocysts as they did before.

The initial prejudice in favour of the positive object on day 1 is presumably a result of the pre-training on the positive object, and implies that the animals are immediately aware of a difference between the positive and negative objects. The discrimination improves up to the third day, which is reflected in the rise in R over this period.

CONCLUSIONS

The results obtained above confirm that *Octopus* distinguishes between sources emitting plane polarized light in planes at right angles to each other, and show that this effect is independent of extra-ocular reflexion. There remain other theoretical possibilities of extra-ocular discrimination, but these have been examined by Moody & Parriss (1961), and have been shown to be exceedingly unlikely. It is therefore concluded that the mechanism of discrimination of polarized light is intra-ocular, as suggested by these authors.

SUMMARY

1. The object of the investigation was to show that the ability of *Octopus* to detect the plane of polarization of light does not depend upon differential reflexion from its surroundings.
2. Animals were trained to distinguish between light plane polarized in the vertical plane (normal to the iris slit of the intact animal) and in the horizontal plane (parallel to the slit).
3. The statocysts were then removed, abolishing the normally fixed orientation of the eyes with respect to gravity.
4. After the operation the plane of polarization was set at each trial so as to be either normal or parallel to the iris slit. Because the eyes were now disoriented, there was no longer any constant relation between these planes and the fixed reflecting surfaces of the aquarium.
5. The animals, nevertheless, continued to discriminate correctly. It is therefore concluded that detection of the plane of polarization depends upon some intra-ocular mechanism.

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