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REVERSAL OF A VISUAL PREFERENCE IN *OCTOPUS* AFTER REMOVAL OF THE VERTICAL LOBE

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INTRODUCTION

Strong preference differences between two stimuli have been commonly encountered when training octopuses (Young, 1958, 1965*b*; Sutherland & Muntz, 1959). It is impossible to know how far these are innate, but they are present in most individuals and may perhaps reflect basic features of the encoding system. It is therefore interesting that preferences found with touch are reversed after removal of the vertical lobes and also after other operations (Wells & Young, 1968). The present paper reports similar reversal of preference in a simple visual discrimination.

METHODS

Octopuses were kept individually in plastic tanks 27 × 50 × 100 cm. with a home at one end. In some of the tanks the walls were a light cream colour, in others dull grey. The direction of preference to black and white was found to vary with the background.

The figures shown were black or white plastic disks of diameter 4·5 cm., attached to a transparent plastic rod. The figures were introduced successively at the end of the tank remote from the home and moved up and down by hand about three times a second. The octopuses mostly remained within the home when not being tested. If necessary they were restrained between tests by a transparent plastic partition, which was raised shortly before the test. An 'attack' was scored only when the octopus touched the figure, and the time from the beginning of the trial was recorded with a stop-watch. In 'no reward' tests the figure was then simply withdrawn. In the training experiments a small piece of fish was given after attacks at one figure (positive), a 10 V. a.c. shock for the other (negative). The trial was ended after 20 sec. if there was no attack.

Trials were at 5 min. intervals. The unrewarded trials were given in twice daily sessions of five with each figure in a randomized order (Gellerman). The 'no reward' animals were fed with a crab after each session. Training was in sessions of eight with each figure, given alternately, with the positive figure first.

Operations for removal of the vertical lobes were performed under urethane anaesthesia. The amount removed was controlled by fixation and sectioning after the experiment. In all the animals reported here more than 80 % of the vertical lobe had been removed. There had been slight damage in some to the underlying subvertical lobe, but as no relevant correlations were detected, the details are not reported.

RESULTS. TESTS WITHOUT REWARD. NORMAL ANIMALS

In white tanks the unrewarded octopuses attacked the black disks more often than the white. The effect was slight; usually there were 40–50 % attacks at white. Occasional animals showed an opposite tendency. Thus in Expt. 1 (Fig. 1 and Table 1), seven animals were tested for forty trials with each figure and all but one showed a

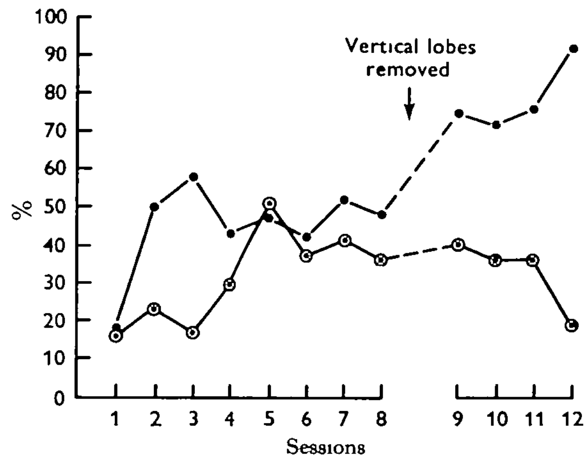

Fig. 1. Expt. 1. Seven octopuses tested without reward before and after removal of the vertical lobes. ●, percentage of all attacks made at white. ○, percentage of attacks to trials. White tanks.

Table 1. *Expt.* 1. *Results of testing seven animals with black and white disks shown randomly without reward in white tanks. Eight sessions of ten trials each before operation, four sessions after removal of the vertical lobes*

	Before operation					After vertical lobe removal			
Session	W	B	W (%)	% att. trails	Session	W	B	W (%)	% att. trials
1	2	9	18	16	9	21	7	75	40
2	8	8	50	23	10	18	7	72	36
3	7	5	58	17	11	19	6	76	36
4	9	12	43	30	12	12	1	92	19
5	17	19	47	51	Total	70	21	76 9	32·5
6	11	15	42	37					
7	15	14	52	41					
8	12	13	48	36					
Total and means	81	95	46·0	31 4					
Octopus									
102	15	17	47	40		4	0	100	10
103	4	8	33	15		2	0	100	5
105	7	11	39	23		3	0	100	7
106	13	17	43	38		17	1	94	45
113	6	9	40	19		13	2	87	38
114	17	13	57	38		20	13	61	83
116	19	20	49	49		11	5	69	40
Mean for individuals			43 9	31·7		70	21	87·3	3 26

black preference, the mean being 44 % for white. In Expt. 2 (Fig. 2 and Table 2) of nine animals tested for twenty trials with each figure only two showed a white preference, the mean being 42 %. There was perhaps a sign of decreasing black preference as the sessions proceeded. The proportion of attacks to trials did not decline consistently over the sessions. Taking Expts. 1 and 2 together the black preference is significant at $P = < 0{\cdot}01$.

In Expt. 3 (Figs. 3 and Table 5) ten animals were first tested for twenty trials with each figure in grey tanks and then transferred to white ones for a similar number

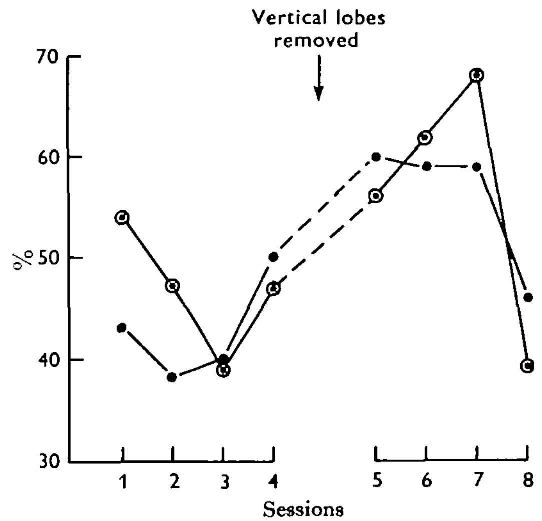

Fig. 2. Expt. 2. Nine octopuses tested as in Expt. 1.

Table 2. *Expt. 2. Nine octopuses tested as in Expt. 1 but for four sessions before and four after removal of the vertical lobes. White tanks*

	Before operation				After vertical lobe removal			
Session	W	B	W (%)	% att. trials	W	B	W (%)	% att. trials
1	21	28	43	54	30	20	60	56
2	16	26	38	47	33	23	59	62
3	14	21	40	39	36	25	59	68
4	21	21	50	47	16	19	47	39
Totals and means	72	96	42·9	46 7	115	87	56·9	56·1
Octopus								
101	8	17	32	63	8	18	31	65
104	14	17	42	83	13	7	65	50
115	5	11	31	40	14	14	50	70
130	8	8	50	40	6	8	43	35
221	5	7	42	30	11	1	92	30
223	14	12	54	65	19	16	54	88
224	5	12	29	43	17	9	65	65
310	8	6	57	35	15	9	63	60
311	5	6	45	28	12	5	71	43
Means for individuals			42·4	47·4			59·3	56·2

more. In the grey tanks there was a slight but definite preference for white (56 %). Three of the animals showed the reverse (but one of these was a very poor attacker). The proportion of attacks declined over the four sessions and the white preference somewhat increased. When transferred to white tanks the group as a whole reversed its preference, which was now in favour of black (44 % attacks at white). The reduction in proportion of attacks at white occurred in all except two of the animals, but not in all of them to the extent of producing an excess of attacks at black. The repeated trials without reward produced progressive extinction, so that by the end of the experiment in white tanks there were attacks at only 25 % of trials. As the attacks fell,

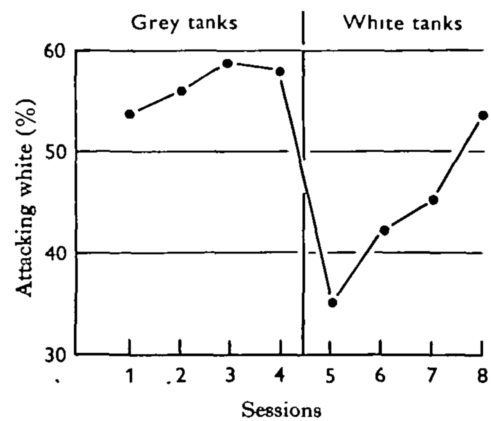

Fig. 3. Expt. 3. Ten normal octopuses tested without reward first on grey and then on white background. (Results by courtesy of G. D. Sanders.)

Table 3. *Expt. 3. Ten octopuses tested as in Expt.* 1, *first for four sessions in grey tanks and then for four in white tanks*

	Grey tanks				White tanks			
Session	W	B	% white	% attacks/ trials	W	B	% white	% attacks/ trials
1	34	29	54	63	13	24	35	37
2	29	23	56	52	13	18	42	31
3	27	19	59	46	13	16	45	29
4	26	19	58	45	14	12	54	26
Totals and means	116	90	56 6	51 5	53	70	43 1	30·7
Octopus								
424	7	0	100	18	0	0	—	0
425	2	1	67	8	1	3	25	10
465	1	3	25	10	0	0	—	0
466	12	14	46	65	10	8	56	45
467	17	17	50	85	8	15	35	58
468	15	9	63	60	8	8	50	40
469	18	10	64	70	9	12	43	53
470	12	3	80	38	3	3	50	15
471	16	18	47	85	9	8	53	43
472	16	15	52	77	5	13	28	45
Means of individuals			56	52			44	31

the proportion of them made at the white disk increased and at the last session was over 50 %.

In addition to these three experiments with long series of tests, smaller numbers of tests (3–15 with each disk) were given to thirty further normal octopuses in white tanks. These made a total of forty-eight attacks at white, 112 at black (33 % white). All but two of the animals attacked black the more often ($P = < 0{\cdot}01$). Attacks were made at 54 % of all trials. The preference for black in white tanks is therefore distinct but not very strong. It manifests itself most when the tendency to attack is strong.

TESTS WITHOUT REWARD

Reversal of preference after removal of the vertical lobes

This was shown by continuation of Expts. 1 and 2, and by tests of a further twenty-four animals only after operation. In Expt. 1 after removal of the vertical lobes the seven animals of Table 1 and Fig. 1 went immediately from about 50 % to over 70 % preference for white, increasing later to 90 % (Table 1 and Fig. 1). The effect is therefore not simply one that is seen immediately after operation. All seven animals showed it strongly.

The nine animals of Fig. 2 and Table 2 went from about 50 to 60 % in favour of white. At the last session they showed a black preference but the level of attack had then fallen very low. Two of the animals did not show the change of preference after operation but the number of attacks of one of these was very low.

The tests on twenty-four further animals after operation gave 136 attacks at white, 103 at black (57 %). Six of them did not show the white preference but in all of these the difference was very small and the total of attacks few. The proportion of attacks altogether in this group was low (38 % of all trials).

The change of preference after operation is therefore marked in most animals but may be absent. It is sometimes associated with an increased tendency to attack after operation (e.g. in Expt. 2), but this increase is by no means uniform. It was absent in Expt. 1 and the animals tested only after operation attacked less than the thirty normal octopuses tested comparably. Previous work has also shown irregular changes of attack tendency after this operation (Young, 1965*b*).

PREFERENCES AS SHOWN BY TRAINING NORMAL ANIMALS

Eight animals trained with black positive in white tanks (Expt. 4) showed an excess of attacks at this figure from the first session onward (Fig. 4). In subsequent sessions they increased the proportion of attacks at the black and decreased those at the white.

The five animals trained in the opposite direction (Expt. 5) made more attacks at the black (negative) than at the white figure throughout the first session (Fig. 4). They attacked the positive (white) disk at only 5 % of trials at first. The difference between numbers of attacks at the positive figure in the first session with training in the two directions is significant at $P < 0{\cdot}05$. In the following sessions those with white positive rapidly increased the proportions of attacks at the positive and decreased them at the negative. From the fourth session onwards there was little difference between the two groups. Both reached an asymptote of 85 % correct responses, attacking their positive disks at about 80 % of trials.

PREFERENCES SHOWN BY TRAINING AFTER REMOVAL OF THE VERTICAL LOBES

Two sets of animals were trained after removal of the vertical lobes, six with black positive but only three with white positive (Expts. 6 and 7). In the early sessions the white was strongly preferred. Those with white positive scored 75 % and 67 % correct in the first two sessions, those with black positive only 46 % and 52 % ($P < 0.05$). Thereafter those with black positive came to attack it more often, whereas those with the white actually reduced their attacks. Both groups ended with about 65 % correct. As usual without vertical lobes the performances were irregular and there are not sufficient animals to make further details worth recording.

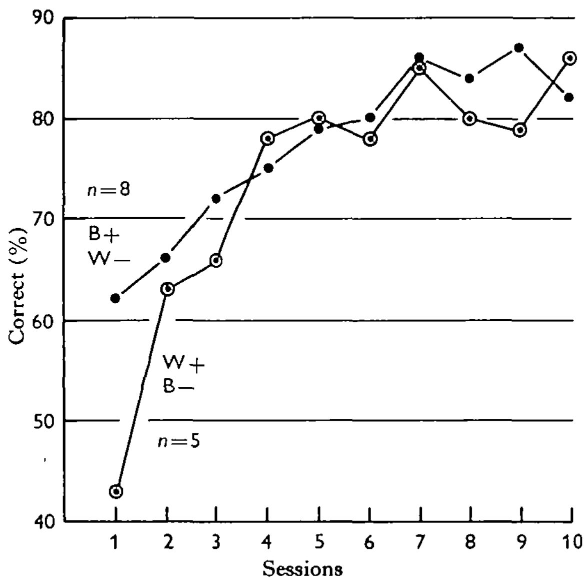

Fig. 4. Expts. 4 and 5. Results of training octopuses to discriminate between black and white either with black disk positive (filled circles), or white disk positive (open circles). White tanks

DISCUSSION

The preference of normal animals for a black disk moving on a white ground is presumably related to the contrast, this figure being more effective in setting up sufficient impulses to initiate an attack than is a white one. This is confirmed by the absence (or reversal) of the difference when the figures are on a grey ground. Clearly, however, the system is not simply one in which the disks stimulate attack unconditionally. It can learn to increase or decrease the attacks at either figure. Therefore some means for setting up encoded representations must be present. There may be distinct classifying cells recording black and white and potentially connected with outputs producing either attack or retreat. It has been suggested that the learning consists in switching off the unwanted pathways (Young, 1965*a*, *b*).

The fact that there are 'preferences', however arrived at, but perhaps innate, between so many visual and tactile alternatives may be a feature that makes for economy in coding. If the system is biased so that the more commonly occurring sensory situations elicit a response that is usually favourable, then it only has to learn the appropriate response to rarer events ('encoding the unexpected' Miller, 1968).

The striking fact for the octopus is that both visual and tactile preferences are reversed after removal of the vertical lobes. Animals without vertical lobes often attack more persistently than normals but the reversed preference is not necessarily associated with an increase in attack.

Reversal of tendencies after this operation has been seen in other circumstances (in addition to the change of tactile preference). It was early noticed that individuals that attacked seldom before operation did so frequently after and vice versa (Young, 1958). Part at least of the significance of the vertical lobes seems to be in regulating both the level of tendency to act (i.e. attack or draw in) and the relative tendencies released by different afferent signals. The memory is thus based upon unequally weighted systems of response, the balances between them being maintained and varied by the numerous small cells of the vertical lobe.

SUMMARY

1. Normal octopuses tend to attack a black disk more often than a white one, when they are shown against a white background.

2. The difference is not present with a grey background.

3. After removal of the vertical lobe the preference is reversed and attacks are now more frequent at a white than at a black figure, when on a white ground.

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