

THE INFLUENCE OF PREOPERATIONAL TRAINING ON  
THE PERFORMANCE OF OCTOPUSES FOLLOWING  
VERTICAL LOBE REMOVAL

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INTRODUCTION

Removal of the vertical lobe from the brain produces no obvious deficiencies in the behaviour of octopuses in aquaria until attempt is made to train them to make visual or tactile discriminations (Boycott & Young, 1950; Wells & Wells, 1957*a*). It is then found that animals operated in this way learn less readily than controls; more trials are required to train them to recognize objects seen or touched and the proportion of errors made, even after prolonged training, is rarely as low as that made by controls. The difference between controls and operated animals is most marked in the case of difficult discriminations, and when training trials are relatively far apart (Boycott & Young, 1955, 1957; Wells & Wells, 1957*a*), so that the performance of animals with the vertical lobe removed most closely resembles that of controls when they are trained to make easy discriminations by means of trials at short intervals. Partial removal of the vertical lobe produces deficiencies dependent upon the proportion of this tissue removed (Boycott & Young, 1955, 1957; Wells & Wells, 1957*a*). These findings indicate that the function of the vertical lobe is, in general, similar in visual and tactile learning.

It should be borne in mind, however, that most experiments on postoperational visual learning have been made with animals trained before operation, whereas postoperational tactile learning has been studied exclusively with animals that were untrained when operated. Since no experiments had been made to determine the effect of vertical lobe removal on the performance of trained animals in tactile discriminations, the justification for comparing visual and tactile experiments was questionable. The present account is of experiments made to rectify this position and deals with the postoperational performance of animals trained to make tactile discriminations before removal of their vertical lobes. By comparing the performance of such animals with that of animals trained after operation without pretraining various conclusions can be drawn about the function of the vertical lobe in tactile learning.

MATERIAL

*Octopus vulgaris* Lamarck of between 300 and 800 g. from the Bay of Naples were used in this work. The animals were caught and kept in individual tanks as described by Boycott (1954) and fed upon crabs or pieces of fish, those showing signs of

damage due to rough handling at capture or failing to feed regularly being discarded.

Animals were blinded by section of the optic nerves (as described in Wells & Wells, 1956) before use in training experiments. Most of them were subjected to a further operation in which parts of the vertical and superior frontal lobes were removed either before training, or in the course of training experiments as described below; these operations to the central part of the brain were carried out as described in Wells & Wells (1957*a*).

In order to ensure complete vertical lobe removals, the lesions were deliberately made large, particularly at the anterior end of the vertical lobe where a small portion of it runs under the superior frontal lobe. Inevitably the superior frontal lobe was partially damaged in many of the animals, and in some cases the whole of this lobe was removed to ensure complete vertical lobe removal. After damage to the lateral parts of the superior frontal lobe, octopuses may fail to attack objects seen at a distance in visual experiments (Boycott & Young, 1955), but there is apparently no effect on the performance of animals in tactile training; indeed, as will be shown in a later account, removal of the superior frontal, vertical and at least a large part of the basal lobes produces animals whose performance in tactile training experiments cannot be distinguished from that of animals lacking only the vertical lobes. As a result, it has been possible to ensure that almost every 'animal lacking the vertical lobe' used in the present series of tactile experiments had the vertical lobe entirely removed, a fact that must be borne in mind when comparing these experiments with visual discrimination experiments (Boycott & Young, 1956, 1957) in which nearly all the animals used had incomplete lesions as a consequence of the operator's anxiety to avoid damage to the lateral parts of the superior frontal lobe.

Animals were killed after use in one or more experiments, and the extent of brain lesions estimated from serial sections prepared according to a modification of Cajal's method given in Sereni & Young (1932).

In the text individual animals are referred to by the number with which they were identified in our original protocols, e.g. C28NVB. The prefix C shows that the experiments were made in 1956 and D, 1957. The suffixes B, NV and NSF denote 'blind' (=optic nerves cut), 'no vertical lobe' and 'no superior frontal lobe' respectively. The categories 'no vertical lobe' and 'no superior frontal lobe' include animals having considerable areas of these parts still intact as well as those in which the lesion was complete.

#### METHOD

Animals were trained as described in Wells & Wells (1956). Briefly, the training consisted of a series of trials at each of which one or other of a pair of Perspex objects was presented, the animal being rewarded with a piece of fish for passing the 'positive' object to the mouth and given a small (6-9 V. a.c.) electric shock if it did the same to the 'negative' object. The animals were given no pretraining experience of the objects. In the present series animals were required to learn to discriminate between a smooth Perspex cylinder, P4, 2.5 × 3.0 cm. long and a

similar cylinder with grooves cut into it, either P1 or P8. P1 had 1 mm. deep grooves cut into it longitudinally at intervals of 3 mm., P8 had similar grooves circumferentially at 2 mm. intervals. When required to discriminate between P1 and P4, controls made about twice as many errors as in P8/P4 discriminations (Wells & Wells, 1957*a*).

Trials were arranged in a systematized order, the interval between trials being either 1 hr. ('long-term' experiments) or 5 min. ('short-term' experiments). Under the long-term conditions there were 8 trials a day (4+, 4-) arranged + - + - + + - - first day, - + - + + - - + second day and so on; the short-term trials were arranged in groups of 20 trials (10+, 10-), always in the order + - + - + + - - + - + - + + - + - + - + -, there being two such groups per day, the second group beginning not less than 6 hr. after the start of the first. In both cases there was an interval of about 14 hr. between the last trial on one day and the first on the next. In the retention tests trials were arranged as in the short-term experiments but no punishments or rewards given.

#### EXPERIMENTAL RESULTS

##### (1) *Train-operate-train experiments made under the long-term conditions*

For these, animals were trained at a rate of 8 trials per day for 6 or 12 days (48 or 96 trials), operated upon at the end of the last day of training, allowed 1 day to recover, and first tested for effects of vertical lobe removal 36 hr. after the operation. Preoperational breaks in training of this length cause little or no deterioration in performance (Table 1).

Six animals were treated in this way, three being trained for 48 and three for 96 trials before operation. All had lesions including complete removal of their vertical lobes. At the end of preoperational training the performance of these animals was nearly perfect, only three errors being made by six animals in the last 2 days (= a total of 96 trials) of their training (Table 1). It is convenient for purposes of comparison with others to express this result in terms of an 'index of differential response' used by Boycott & Young for comparing the performance of animals in visual experiments. This index ('*I*') has the advantage of making it possible to compare the performance of animals whether they err predominantly by accepting the negative objects (as here) or by rejection of the positives, and is calculated by dividing the difference in number of acceptances of the positive and negative objects by the total number of trials with each.  $I = 0.0$  indicates random errors,  $I = 1.0$  perfect performance. Over the last 2 days (= 96 trials; 48+, 48-) of their preoperational training, the value of *I* for the six animals given in Table 1 was  $(48 - 3)/48 = 0.94$ .

When training was continued after operation it was found that the same animals at first took all the objects, both positive and negative, as at the start of their preoperational training, so that for the 2 days (96 trials) immediately after operation  $I = 0.04$ . Although these animals subsequently relearned to discriminate between the objects they were slower to do this than in their original preoperational

Table 1. Train-operate-train experiments

(Eight trials (4+, 4-) per day. Discrimination between P4 and P8. The results with each animal are arranged in three columns; under + and - are given the number of times that the positive and negative objects were taken on each day. Column E gives the total daily errors.)

Proportion of vertical lobe removed	Trained for 48 trials before operation						Trained for 96 trials before operation														
	C68NVB NSF			C69NVB NSF			C70NVB NSF			C26NVB NSF			C27NVB NSF			C28NVB NSF					
	100 %			100 %			100 %			100 %			100 %			100 %					
	+	-	E	+	-	E	+	-	E	+	-	E	+	-	E	+	-	E			
	4	4	4	4	1	1	4	4	4	4	2	2	4	3	3	4	2	2			
	3	3	4	4	2	2	3	2	3	3	1	2	4	2	2	3	1	2			
	4	0	0	4	0	0	4	2	2	4	0	0	4	0	0	4	1	1			
	4	1	1	4	0	0	4	1	1	4	0	0	4	0	0	4	0	0			
	4	0	0	4	0	0	4	1	1	4	1	1	4	0	0	4	0	0			
	4	0	0	4	1	1	4	0	0	4	1	1	4	1	1	4	1	1			
	Operation, vertical lobe removed. 36 hr. break						36 hr. break in training														
	4	4	4	4	4	4	4	4	4	4	1	1	4	0	0	4	0	0			
	4	4	4	4	4	4	4	4	4	4	3	3	4	0	0	4	2	2			
	4	4	4	4	4	4	4	4	4	4	1	1	4	0	0	4	0	0			
	4	3	3	4	2	2	4	3	3	4	0	0	4	0	0	4	0	0			
	4	1	1	4	3	3	4	4	4	4	0	0	4	0	0	4	1	1			
	4	1	1	3	4	5	4	4	4	4	0	0	4	0	0	4	0	0			
	36 hr. break in training						Operation, vertical lobe removed. 36 hr. break														
	4	4	4	3	2	3	4	1	1	4	4	4	4	2	2	4	4	4			
	4	0	0	2	1	3	4	2	2	4	4	4	4	4	4	4	4	4			
	4	1	1	1	0	3	4	3	3	4	4	4	4	1	1	4	2	2			
	4	1	1	1	1	4	4	0	0	4	4	4	4	0	0	4	3	3			
	4	2	2	3	2	3	4	2	2	4	3	3	4	0	0	4	2	2			
	4	1	1	3	1	2	4	2	2	4	2	2	4	0	0	4	2	2			
	36 hr. break in training						36 hr. break in training														
	4	0	0	3	1	2	4	3	3	4	2	2	4	0	0	4	2	2			
	4	3	3	4	0	0	4	2	2	4	1	1	4	0	0	4	2	2			
	4	3	3	3	0	1	4	1	1	4	1	1	4	0	0	4	1	1			
	4	1	1	3	0	1	4	0	0	4	1	1	4	0	0	4	0	0			
	4	1	1	3	0	1	3	0	1	4	2	2	4	0	0	4	0	0			
	.	.	.	.	.	.	.	.	.	4	0	0	4	0	0	4	0	0			
	Index of differential response for the whole period of training																				
	1. Before operation			0.63			0.83			0.54			0.75			0.88			0.81		
	2. After operation			0.50			0.34			0.41			0.44			0.85			0.54		
	Index for the first 2 weeks postoperational training																				
	0.46			0.15			0.29			0.44			0.85			0.54					

training (Table 1), a result which suggests that very little trace of the preoperational discrimination training survives vertical lobe removal. It is only when the performance of such animals is compared with that of others trained after operation without pretraining, that traces of preoperational learning can be seen to survive vertical lobe removal. The index of differential response for the first 2 weeks of postoperational training of the six pretrained animals shown in Table 1 was 0.46;

Table 2. *Train-operate-train experiments*

(Training at 40 trials per day in two groups of 20 (10+, 10-); for retention tests with these animals see Wells & Wells (1958). Discrimination between P1 and P4. Conventions as Table 1.)

Proportion of vertical lobe removed	C173NVB NSF			C188NVB NSF			C189NVB		
	100%			100%			70%		
	+	-	E	+	-	E	+	-	E
	9	9	10	9	6	7	10	6	6
	10	5	5	10	6	6	9	3	4
	10	2	2	10	3	3	10	3	3
	9	0	1	10	4	4	10	0	0
	9	0	1	10	2	2	9	0	1
	10	1	1	10	3	3	10	1	1
	Operation, vertical lobe removed. 36 hr. break in training								
	10	1	1	10	2	2	10	4	4
	7	0	3	10	1	1	7	1	4
	.	.	.	10	5	5	10	3	3
	.	.	.	10	2	2	7	3	6
	.	.	.	10	3	3	10	1	1
	.	.	.	10	2	2	9	1	2
	.	.	.	.	.	.	7	3	6
	.	.	.	.	.	.	7	2	5
	Index of differential response for the whole period of training								
1. Before operation	0.67			0.58			0.75		
2. After operation	0.80			0.75			0.61		

the index for the same period for seven animals without pretraining was 0.39 (details of the performance of these seven animals, all of which—save one with 95% removed—had the vertical lobe entirely removed, are given in Wells & Wells, 1957*a*). The difference between pretrained and non-pretrained animals was more marked in the case of those pretrained for 96 than for 48 trials; for the 2 weeks after operation  $I$  (mean) = 0.60 for three animals each trained for 96 trials before operation, and  $I$  (mean) = 0.31 for three animals trained for 48 trials.

(2) *Train-operate-train experiments made under the short-term conditions*

Results rather different from the above are obtained when animals are pretrained at a rate of 40 instead of 8 trials per day. Table 2 shows the performance of three animals each of which was trained for 120 trials before removal of its vertical lobe during a 36 hr. break in training. On the last day before operation these three animals made nine errors in a total of 120 trials ( $I = 0.85$ ), and in a similar period immediately after removal of their vertical lobes fifteen errors ( $I = 0.75$ ). The decline in performance produced by the operation ( $I = 0.85$  to  $I = 0.75$ ) is obviously not of the same order as that produced in comparable experiments made under the long-term conditions (where the index fell from 0.94 before operation to 0.04 afterwards), although the number of pretraining trials per animal was not dissimilar in the two cases (120 trials under the short-term conditions compared with up to 96 trials under the long). It should be noted that the animals were trained to discriminate between

P1 and P4 in the short and P8 and P4 (an easier discrimination, see p. 326) in the long-term experiments. Removal of the vertical lobe is known to have a relatively greater effect upon the performance of animals in the more difficult P1/P4 discrimination (Wells & Wells, 1957*a*); so that had the objects been alike in the two sets of experiments, the difference produced in the results would have been even more marked.

(3) *Train-operate-retain experiments*

In the long-term experiments described in §1 above, little trace of pretraining was detectable immediately after removal of the vertical lobe, while the short-term experiments reported in the last section show that under somewhat different conditions (trials five times as frequent) considerable traces of pretraining survive the operation. The long-term experiments alone might lead one to suppose that learning normally takes place almost entirely within the vertical lobe and only elsewhere if this is not present. The short-term experiments clearly show that the structural and organizational changes occurring as a result of training are not limited to the vertical lobe, and, indeed, that its removal causes very little immediate loss of memory under these conditions.

One possible explanation of this would be that the training conditions dictate where in the nervous system learning takes place, and that for some reason training at a rate of 40 trials per day produces changes that are either more widespread or limited to a different part of the nervous system than training at a rate of 8 trials per day. Another possibility is that learning takes place in the same part of the brain in the two cases, but that the long-term conditions do not reveal memories that can be shown to be present under the short-term conditions. To check this, animals were trained under the long and short conditions, operated as before, and, after the usual 36 hr. gap, subjected to identical retention tests. These were carried out in the same order as under the short-term training conditions but without reward or punishment.

The results of retention tests are given in Tables 3 and 4. Control animals were subjected to dummy operations in which they were anaesthetized and the brain exposed as usual, but no lesion made. Table 3 gives the results of retention tests made with six animals (four having vertical lobe lesions and two controls) after training to distinguish P8 from P4 under the long-term conditions. During the last 16 trials (2 days) of their preoperational training  $I=0.88$  for these six animals. In post-operational retention tests of 20 trials made 36 hr. later, the performance of one control was perfect ( $I=1.0$ ) and the other nearly so ( $I=0.90$ ). The four operated animals made a considerably higher proportion of errors, mainly by acceptance of negative objects ( $I=0.60, 0.10, 0.30, 0.40$ —mean 0.35). The performance of these animals, although poorer than that of the controls, clearly shows some retention of the preoperational training.

Table 4 gives results of a similar series of tests carried out after short-term training to discriminate between P1 and P4 or between P8 and P4. The length of pretraining in these experiments was somewhat variable as the animals were trained not for a given number of trials, but to a prescribed standard of accuracy

Table 3. *Train-operate-retain experiments*

(Pretraining at 8 trials (4+, 4-) per day, retention tests of 20 trials (10+, 10-) at 5 min. intervals without shocks or rewards. Discrimination between P8 and P4. Conventions as Table 1.)

	C132B			D9B			D1NVB			D2NVB NSF			D4NVB			D8NVB		
Proportion of vertical lobe removed	.			.			80%			100%*			90%			100%		
	+	-	E	+	-	E	+	-	E	+	-	E	+	-	E	+	-	E
	4	4	4	3	3	4	4	4	4	4	2	2	2	3	5	2	1	3
	4	2	2	4	1	1	4	4	4	3	1	2	3	1	2	3	0	1
	4	1	1	4	1	1	4	2	2	4	0	0	4	2	2	3	0	1
	4	2	2	4	1	1	4	2	2	4	0	0	4	0	0	4	0	0
	4	0	0	4	2	2	4	1	1	4	0	0	4	0	0	4	0	0
	4	1	1	4	0	0	4	1	1	4	0	0	4	2	2	4	0	0
	Dummy op.						Operation, vertical lobe removed.											
	36 hr. break in training																	
	4 1 1			Retention tests														
	4	0	0	10	0	0	10	6	6	10	9	9	10	3	3	8	2	4
	4	0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	4	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	4	0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	4	0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Dummy op.																	
	36 hr.																	
	Retention																	
	9	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

\* Since the entire superior frontal lobe was removed, disconnecting the vertical lobe from its tactile input (Boycott & Young, 1955) D2NVBNSF may be regarded for purposes of comparison as having the vertical lobe entirely removed, although a part of the extreme right-hand gyrus (about 15% of the total volume of the lobe) remained after operation.

before operation.\* Each animal was trained under the short-term conditions until it reached a criterion of 85% correct responses in a group of 20 trials. It was then overtrained for as many trials as it had taken to reach this standard and then operated. Retention tests were carried out as before, 36 hr. after the end of training. In these tests two controls trained to discriminate between P1 and P4 made 1 and 2 errors respectively ( $I=0.90$  and  $0.80$ ); five animals without their vertical lobes made between two and eight errors each (average 5.4 errors,  $I=0.46$ ) and two trained to distinguish between the easier P8 and P4 made five and eight errors ( $I=0.50$  and  $0.20$ ).

#### DISCUSSION

The effect of preoperational training on the performance of octopuses when training is continued after complete removal of their vertical lobes is summarized in Fig. 1. This shows that:

(1) Removal of the vertical lobes from animals pretrained under the long-term conditions leads to an immediate decline in performance. When training is

\* With one exception, C132NVB, that had already been trained as a control in the long-term experiments.

Table 4. *Train-operate-train under the short-term conditions*  
(Conventions as Table 1.)

Proportion of vertical lobe removed	Trained on P1/P4							Trained on P8/P4	
	C158B*	C171B	C149NVB NSF	C151NVB	C154NVB NSF	C155NVB NSF	C158NVB* NSF	C132NVB† NSF	C202NVB NSF
			95%	100%	100%	100%	100%	95%	90%
	+ - E	+ - E	+ - E	+ - E	+ - E	+ - E	+ - E	+ - E	+ - E
	10 9 9	6 6 10	10 10 10	8 8 10	10 9 9	8 1 3	10 3 3	10 0 0	5 5 10
	10 4 4	9 3 4	10 6 6	5 0 5	10 6 6	9 2 3	10 4 4	10 0 0	2 1 9
	10 2 2	10 3 3	8 0 2	9 1 2	10 5 5	Vert. out.	10 0 0	10 0 0	7 4 7
	10 0 0	9 1 2	10 1 1	7 3 6	10 2 2	36 hr. break	Vertical lobe removed	10 4 4	10 4 4
	10 1 1	4 1 7	8 0 2	6 0 4	10 2 2	3 0 7	36 hr. break in training	10 2 2	10 0 0
	10 0 0	6 1 5	6 0 4	5 0 5	10 2 2	. . .	10 4 4	10 0 0	10 0 0
	Dummy operation		Vertical lobe removed	Vertical lobe removed	Vert. out.	. . .	. . .	10 2 5	Vert. out.
			36 hr. break in training	36 hr. break in training	36 hr. break	. . .	. . .	7 2 5	36 hr. break
	10 1 1	10 2 2	3 1 8	10 2 2	10 6 6	. . .	. . .	. . .	3 1 8
	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .
	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .

\* Same animal. Training in right-hand column immediately follows last retention test on left-hand column.  
† This animal had previous training as shown in Table 3.



continued, however, the accuracy of response approaches that attained preoperationally.

(2) Under these conditions animals that had not been trained before operation required more trials to reach a given standard of accuracy of response postoperationally than pretrained animals.

(3) Removal of the vertical lobes from animals after pretraining under the short-term conditions causes little or no disturbance to the postoperational performance of these animals.

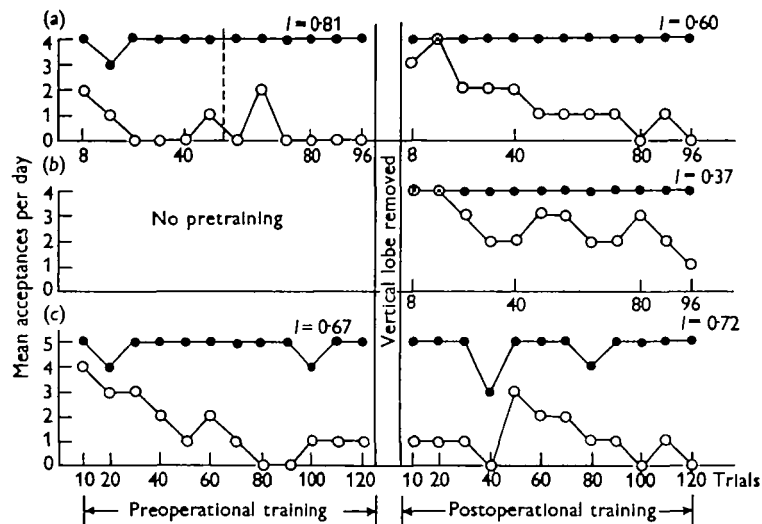


Fig. 1. Effects of a similar number of trials of preoperational training at 8 and 40 trials per day on the postoperational performance of animals following removal of their vertical lobes. (a) 3 NV animals; train-operate-train under the long-term conditions of 8 trials per day. (b) 6 NV animals; operate-train under the same conditions. (c) 3 NV animals; train-operate-train under the short-term conditions of 40 trials per day. ●, positive object; ○, negative object. Vertical dotted line indicates break in training of 36 hr. There was a similar break after vertical lobe removal.

These results show that some effects of both long- and short-term pretraining survive vertical lobe removal, and thus confirm the results of retention tests (Tables 3 and 4) showing postoperational survival of memories ensuring distinct responses to the test objects after long- or short-term pretraining.

Whatever changes to the structure or organization of their nervous systems have occurred as a result of training, these changes are not limited to the vertical lobe. If this is so, why are the responses of these animals less accurate after vertical lobe removal? We can show, by using animals operated without pretraining, that under suitable conditions those parts of the nervous system outside the vertical lobe are capable of forming and maintaining memories ensuring an accuracy of response equal to that of unoperated animals, at least in simple discriminations, although rather more trials are required to reach this state than when the vertical lobe is present (Wells & Wells, 1957*a*). When this is considered, together with the results

of the present series of experiments, which show a partial loss of learned responses after operation and subsequent recovery when training is continued, several possible ways in which the vertical lobe may be contributing to the learning process can be envisaged.

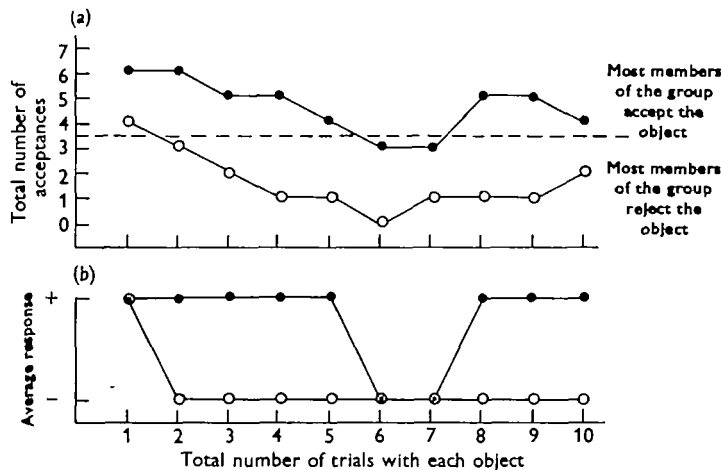


Fig. 2. Detail of the results of the retention tests with operated animals shown in Table 4. Each retention test consisted of 20 trials in the order  $+ - + - + - + - + - + - + - + -$ . ●, indicates positive; ○, the negative object. (a) gives the total number of times that the seven animals tested took each object at each trial. The ratio of positive to negative objects taken by the group remained about the same throughout the 20 trials of the retention test, although the total number of objects taken at each trial became less as the test progressed. (b) gives the same results considered in an all or nothing manner (i.e. whether the group, considered as a whole, reacted positively or negatively to the object presented at each trial). It can be seen that a distortion of the true result is produced, giving the impression that the animals failed to discriminate in some trials and succeeded in others, whereas (a) clearly shows that the animals discriminate between the objects to about the same extent throughout the experiment. Analogous distortions are inherent in discrimination experiments in which the degree to which animals can separate objects is concealed because they must react to them in an all or nothing manner (see text).

Previous workers have drawn attention to the fact that in many experiments vertical lobe removal is followed by an increase in the number of attacks made in situations that the animals had learned to avoid preoperationally. Sutherland (1957) has suggested that in visual discriminations the vertical lobe has a mainly inhibitory function, serving to keep a balance between positive and negative responses that is lost when this part is removed. Boycott & Young (1956, 1957) and Young (1956), again on a basis of the results of visual experiments, take the view that the vertical lobe is not so much concerned with an over-all inhibition of the 'positiveness' of response as with the formation of memories preventing attack. On the face of it, these views are supported by the tactile experiments described in this account, in all of which there is seen a tendency to err by reacting positively towards all the objects touched after vertical lobe removal. On the other hand, an exactly similar condition is found in *untrained* animals, which typically take all objects presented to them at the start of tactile training experiments (Wells & Wells, 1956, 1957*b*), and

in trained animals subjected to retention tests after breaks in training of from 5 to 10 days (Wells & Wells, 1958). Moreover, the ratio of errors made by accepting negative objects to errors by rejection of positives is found to be similar in controls and in animals lacking the vertical lobe, both of which err predominantly by acceptance of the negative objects in tactile training (Wells & Wells, 1957*a*). Taken together, these facts indicate that the tendency to positive responses following removal of the vertical lobes in tactile experiments may be attributable to a lack of effective memories of any sort rather than to a lack of memories specifically connected with negative responses.

The present authors do not believe that the facts so far available justify the assumption that the vertical lobe has a different function in the case of positive and negative memories, and suggest that its presence merely serves to increase the mass of nervous tissue available for memory retention without in any way altering the sort of memories that can be retained. If this is so, then its removal might be expected to obliterate 'positive' and 'negative' memories equally.

The nervous system of a single animal may be regarded as a population of neural units whose individual effects summate to produce the responses we observe. If the conditions of a discrimination experiment dictate that responses must be either 'positive' or 'negative', the results obtained can only record the condition of the animal's nervous system in a form such as that given in Fig. 2*b*, which is necessarily a distortion of the truth. When this is taken into account, apparently paradoxical results like those obtained by postoperational retraining and retention tests become comprehensible. In the experiments in Table 1, where long-term training was continued after operation, the animal at first took all the objects, which could be interpreted as showing that no memories permitting separation of the objects survive the operation. Yet when retention tests are carried out after operation instead of continued training, clear evidence that such memories do survive the operation is obtained. To explain this we need only suppose that the animal's positive responses to the negative objects are in some way less positive than its responses to the positive objects in both experiments. This difference is not at first revealed under the training conditions in which rewards and punishments are given, possibly because feeding the animals tends to raise their tendency to react positively as Young (unpublished) has shown in visual experiments. Under the retention test conditions, however, the animals' tendency to react positively to objects of both sorts is lowered as a result of repeating unrewarded actions until the weaker positive response to the negative object becomes ineffective.\*

There is naturally no sharp transition between weak and strong memories, and in experiments in which attempt has been made to rate the degree of reaction as, for example, by timing the delay before attacking in a repeated and rewarded situation (Boycott & Young, 1950, 1956), it has been shown that the delay before attacking

\* When a series of retention tests is made with an animal that at first reacts positively towards both of the objects, it is usual to find a progressive fading of positive responses, first to the negative and then to the positive object. In such series it is therefore usual to find a reduction in the proportion of errors made over the first few groups of trials (animal takes fewer negatives), followed by an increase as the animal begins to reject both objects (Wells & Wells, 1958).

decreases steadily as memories of specific situations become better and better established. The strength of a memory—as rated by the increase in probability of a particular type of reaction in a particular situation as a result of experience—will depend upon the cumulative effects of past experience and the time elapsed since the last occurrence of that situation. A memory becomes established throughout considerable masses of nervous tissue in octopuses as in vertebrates (Boycott & Young, 1950; Lashley, 1950) and it seems reasonable to suppose that the effectiveness or strength of a memory depends upon the total mass of cells or units available. Removal of a proportion of these would produce a proportional weakening of the memory concerned, making it statistically less likely to influence motor reactions to stimuli in any particular way. The authors regard removal of the vertical lobe as reducing the amount of memory-containing tissue in this way. Memories acquired as a result of preoperational training become weakened, and residual memories left elsewhere in the nervous system can only be revealed by altering the state of the animal as has been described above. The effect of further training summates with these residual (sometimes in themselves ineffective) memories, and in long-term discrimination experiments it is only possible to detect their postoperational survival by comparing the performance of pretrained and unpretrained animals. It should be noted, however, that because the capacity of the whole system has been permanently reduced by the operation, the standard of accuracy of responses may never reach that attained preoperationally. This is likely to be particularly evident in the case of difficult discriminations—those in which even the best established memories scarcely permit controls to separate situations to be discriminated with regularity—so that one would expect to find a relation between the difficulty of the most difficult discrimination that can be learned and the proportion of vertical lobe remaining under any given set of training conditions. Evidence from visual and tactile discrimination experiments indicates that this is so (Boycott & Young, 1957; Wells & Wells, 1957*a*). Since the strength of a memory depends among other things upon the length of time since it was last reinforced, (*a*) the performance of animals in any given discrimination and (*b*) the most difficult discrimination that an animal can be taught to make will also depend upon the interval between trials, so that it should prove possible to compensate for vertical lobe removal to some extent by placing trials closer together. This has also been demonstrated in discrimination experiments (Wells & Wells, 1957*a*).

#### SUMMARY

1. Blind octopuses were trained to discriminate between two objects by touch by taking one and rejecting the other. When they had learned to do this their vertical lobes were removed and postoperational survival of the effects of preoperational training was tested, either by continuation of training or by means of retention tests.
2. When training was continued after vertical lobe removal animals pretrained at a rate of 8 trials per day for 48 or 96 trials reverted to taking both of the objects

to be discriminated (as at the start of training), but subsequently relearned to discriminate between them with an accuracy approaching that of controls. They took fewer trials to learn after operation than animals that had not been pretrained.

3. Animals pretrained at a rate of 40 trials per day for 120 trials showed little or no disturbance of learned responses as a result of the same operation.

4. In retention tests carried out immediately after operation, animals pretrained for a similar number of trials at rates of 8 and 40 trials per day made more errors than controls, but showed, nevertheless, that the effects of pretraining by either method were not entirely lost as a result of the operation.

5. These results are discussed in relation to the general problem of the interpretation of discrimination experiments which force animals to react 'positively' or 'negatively' in an all-or-nothing manner and thereby conceal differences in the degree to which memories are established.

6. It is concluded that the effect of vertical lobe removal can be attributed to a reduction in the amount of tissue available for memory retention.

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#### REFERENCES

- BOYCOTT, B. B. (1954). Learning in *Octopus vulgaris* and other cephalopods. *Pubbl. Staz. zool. Napoli*, **25**, 67-93.
- BOYCOTT, B. B. & YOUNG, J. Z. (1950). The comparative study of learning. *Symp. Soc. Exp. Biol.* **4**, 432-53.
- BOYCOTT, B. B. & YOUNG, J. Z. (1955). A memory system in *Octopus vulgaris* Lamarck. *Proc. Roy. Soc. B*, **143**, 449-80.
- BOYCOTT, B. B. & YOUNG, J. Z. (1956). Reactions to shape in *Octopus vulgaris* Lamarck. *Proc. Zool. Soc. Lond.* **126**, 491-547.
- BOYCOTT, B. B. & YOUNG, J. Z. (1957). Effects of interference with the vertical lobe on visual discriminations in *Octopus vulgaris* Lamarck. *Proc. Roy. Soc. B*, **146**, 439-59.
- LASHLEY, K. S. (1950). In search of the engram. *Symp. Soc. Exp. Biol.* **4**, 454-82.
- SERENI, E. & YOUNG, J. Z. (1932). Nervous degeneration and regeneration in Cephalopods. *Pubbl. Staz. zool. Napoli*, **12**, 173-208.
- SUTHERLAND, N. S. (1957). Visual discrimination of orientation by *Octopus*. *Brit. J. Psychol.* **48**, 55-71.
- WELLS, M. J. & WELLS, J. (1956). Tactile discrimination and the behaviour of blind *Octopus*. *Pubbl. Staz. zool. Napoli*, **28**, 94-126.
- WELLS, M. J. & WELLS, J. (1957a). The effect of lesions to the vertical and optic lobes on tactile discrimination in *Octopus*. *J. Exp. Biol.* **34**, 378-93.
- WELLS, M. J. & WELLS, J. (1957b). Repeated presentation experiments and the function of the vertical lobe in *Octopus*. *J. Exp. Biol.* **34**, 469-77.
- WELLS, M. J. & WELLS, J. (1958). The performance of octopuses in retention tests following tactile discrimination training. (In press.)
- YOUNG, J. Z. (1956). Visual responses by octopus to crabs and other figures before and after training. *J. Exp. Biol.* **33**, 709-29.