

THE EFFECT OF VERTICAL LOBE REMOVAL ON THE PERFORMANCE OF OCTOPUSES IN RETENTION TESTS

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(Received 6 December 1957)

INTRODUCTION

Removal of the vertical lobe from the brain of blind octopuses causes defects in the performance of these animals under training conditions. When such animals were trained postoperationally to make tactile discriminations known to be made readily by blind but otherwise unoperated animals they made many more errors than controls. The effect of vertical lobe removal upon the number of trials required to train octopuses to a given criterion of response was more marked when trials were at intervals of 1 hr. than when trials were at intervals of 5 min., the performance of animals under the latter conditions approaching that of controls (Wells & Wells, 1957*a*). It was concluded that the vertical lobe contributes to the persistence of memories between trials; a similar interpretation of the results of visual discrimination experiments was made by Boycott & Young (1955, 1957). Further experiments, in which the behaviour of animals in the *first* trial of training experiments was particularly considered, showed that removal of the vertical lobe has effects upon the performance of animals that cannot be attributed to failure to retain memories between trials (Wells & Wells, 1957*b*). On a basis of the results of the latter experiments it was suggested that the vertical lobe serves to increase the effect of sensory experience in the establishment of memories during the period in which the sensory input is actually occurring rather than to reduce the rate of decay of memories once set up.

If this were so one would expect to find that memories once established would fade at about the same rate in controls and in animals lacking their vertical lobes. The present account is of retention tests made with controls and 'no vertical' animals that have previously been trained to the same standard of accuracy of response.

MATERIAL AND METHOD

Octopuses of from 250–750 g. from the Bay of Naples were obtained and treated as described by Boycott (1954). Before use in training experiments all the animals were blinded by section of their optic nerves and some of them were subjected to a further operation in which parts of the brain were cut out. Details of operational methods are given in Wells & Wells (1956, 1957*a*). After a postoperational period of several days, during which the octopuses were fed upon pieces of fish but given

no experience of the test objects, training experiments were carried out as described in Wells & Wells (1957*a*).

In these experiments animals were required to learn to distinguish by touch between the members of a pair of Perspex cylinders, one of which was smooth (P₄), the other (P₁ or P₈*) roughened by deep grooves cut into it. Training consisted of a number of trials, at each of which one or other of the objects was presented, the animals being rewarded with a piece of fish for passing the 'positive' object to the mouth, and punished with a small (6 V. a.c.) electric shock if they did the same with the 'negative'. There were 40 such trials per day, in two groups of 20 (10+, 10-) each systematized thus:

+ - + - + + - - + - + - - + + - + - + - .

Individual trials in a group were at intervals of 5 min. and the start of the second group of trials on any day was not less than 6 hr. after the beginning of the first. Under these conditions octopuses speedily learn to discriminate between the test objects, passing the positive object to the mouth and rejecting the negative by thrusting it away to arm's length whenever presented.

For the present series of experiments animals were trained until they attained a standard of either 75% or 85% correct responses (five and three errors or less respectively) in a group of 20 trials and were then overtrained for a similar number of trials. During the period between the cessation of training and the start of retention tests the animals were fed regularly but given no contact with the test objects. No other experiments were made during these periods, so that the animals had no opportunity of tactile experience other than that afforded by their food or contact with the surfaces of their aquaria. Retention test trials were carried out in groups of twenty exactly as in training except that no rewards or punishments were given.

Throughout this account individual animals are referred to by the number with which they were identified in our original protocols. This number is made up of a prefix (B, C or D being 1955, 1956 and 1957 respectively), an individual reference number and a suffix indicating the lesion made. The suffixes appearing here are B=blind (optic nerves cut), NOL=no optic lobes, NV=no vertical lobe, and NSF=no superior frontal lobe. Thus C₁₀NVNSFB indicates a blind animal with a lesion to the vertical and superior frontal lobes, experiment made in 1956. The extent of lesions made was measured from serial sections as described in Wells & Wells (1957*a*).

The vertical lobe lies immediately behind and in some places beneath the superior frontal lobe (Young, 1951) so that it is difficult to ensure complete removal of the former without some damage to the latter. In visual experiments damage to the lateral parts of the superior frontal lobes appears to prevent octopuses from attacking objects seen at a distance, making it difficult or impossible to train them (Boycott & Young, 1955). No such undesirable effects are produced by comparable operations in tactile experiments where the performance of animals with both the

* P₈ had more grooves and was therefore rougher than P₁. Octopuses find the P₁/P₄ discrimination about twice as difficult as the P₈/P₄ (Wells & Wells, 1957*c*). In the present series of experiments all the animals save those listed in Table 4 were trained to discriminate between P₁ and P₄.

superior frontal and the vertical lobes removed appears to be indistinguishable from that of animals lacking the vertical lobe only (Wells & Wells, 1957*a*, 1958). In most of the operations made for the present series of experiments part of the superior frontal lobe was cut away to ensure complete removal of the vertical lobes.

RESULTS

Because of the considerable number of animals involved, it is not practicable to publish details of the training of all the octopuses used in the retention tests reported in this account. The performance of some typical individuals has, however, been recorded in full elsewhere, and references are included in the tables where records of such animals appear.

(1) *Experiments with control animals*

Among the blind controls are included two animals with the optic lobes removed by section of the optic tracts peripheral to the optic tract ganglia; this operation has been shown elsewhere to be without effect on tactile learning (Wells & Wells, 1957*a*). The results of retention tests with these controls are given in Table 1. This table shows that six animals (group A) first tested 5 days after the cessation of training averaged 3.2 errors in a group of 20 trials compared with less than one error in their last 20 training trials. Five of these animals tested again 10 days later averaged 5.2 errors. A second group of four animals (group B), trained to a criterion of 75 % correct responses instead of the usual 85 %, averaged 6.8 errors when first tested for retention at 10 days. In both groups the range of variation (of from 1 to 10 errors) was very great. It should be noted that with one exception (D 11B, 10-day test) animals erred in retention tests predominantly by taking the objects that they had previously been trained to reject. Errors due to failure to accept 'positive' objects were comparatively rare. It has already been pointed out elsewhere (Wells & Wells, 1956, 1957*c*) that in the absence of punishment octopuses tend to revert to taking all small objects that they touch, including those that they have previously been taught to reject.

It is generally possible to demonstrate that such animals still retain memories enabling them to discriminate between objects that they have been taught to distinguish. This is most readily achieved by repetition of retention tests at frequent intervals until the animal ceases to repeat the unrewarded action of taking the objects. It is found in such cases that the positive response to the 'negative' object disappears before the positive response to the 'positive' object, so that there is a transitory improvement in performance during which the animal may make no errors at all.

The process of revealing latent discriminatory memories in retention tests can be accelerated by giving small electric shocks, as used in training, either at each trial (regardless of whether the object presented has been 'positive' or 'negative' in pretraining), or in a group shortly before the beginning of the retention test. An example is given in Fig. 1. This animal (D 3 3 B) made only 1 error in a retention test 5 days after the end of its training, but failed to discriminate at all in a similar

test 10 days later, taking all the objects that were presented. Six hours later the animal was retested, but this time a small (6 V. a.c.) electric shock was given immediately after each of the first 8 trials (4 with the positive object and 4 with the negative). As a result of this treatment only the first two negative objects were taken. After eight shocks the animal began to reject also the positive objects and no further shocks were given, with the result that positive responses to the positive objects but not to the negative objects were resumed.

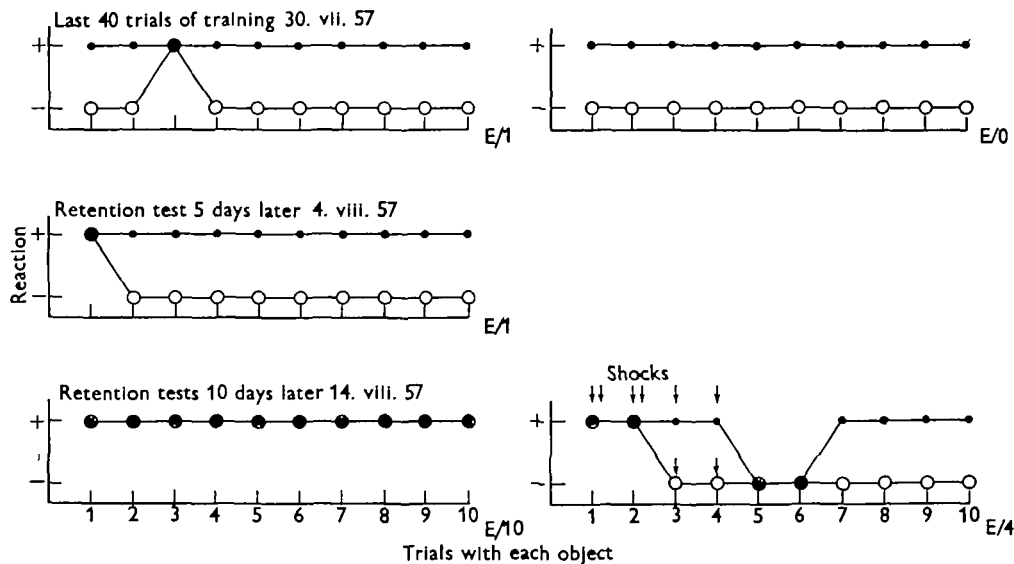


Fig. 1. Detail of the results of a typical series of retention tests; octopus D 33 B. The performance of the animal in the last 40 of 120 training trials is given in full; reactions are recorded as + when the animal accepted the object and as - when it rejected it. Training was followed by an unrewarded retention test 5 days after the end of training, and again 10 days later. In the first set of trials at the end of the second period, the animal took all the objects presented. In a second series 6 hr. later small electric shocks, indicated ↓, were given at the first 8 trials (regardless of the object presented and the animal's reaction to it); this lowered the animal's tendency to respond positively and revealed persistence of the ability to discriminate between the objects.

Other instances where a series of retention tests was made in quick succession, with or without electric shocks, are recorded in Tables 3 and 4. There is a considerable individual variation in the number of trials required to eliminate responses to the test objects but all such series show the same cycle of events (positive response to the negative object fades before the positive response to the positive) as D 33 B.

Results of this sort are perhaps best interpreted as revealing memories of the negative object that are too 'weak' to influence the type of reaction made when the animal is otherwise likely to respond in a strongly positive manner towards objects that it touches. When this tendency is reduced by frequent repetition of unrewarded actions, or by electric shocks, memories at first masked are revealed (Wells & Wells, 1958). Feeding, on the other hand, increases the probability of positive

reaction. In Tables 3 and 4 there are five instances in which animals were fed shortly before retention tests. In four out of these five cases the proportion of objects taken was greater than in the last tests before feeding (normally animals were fed immediately after the completion of each section of tests, so that they were never tested less than four hours after last being fed). In the remaining instances the proportion of objects taken remained the same. Similar effects have been shown in visual experiments where feeding shortly before tests enhances the tendency to react positively and may conceal memories that would certainly lead to discrimination if the animals remained unfed (Young, 1957).

Table 1. Retention tests with control animals trained to discriminate between P1 and P4

(Each test consisted of 20 trials, 10+, 10-. Columns show the number of times that each object was taken and the total errors (column E).)

| | In the final 20 trials of training | | | In retention tests | | | | | | |
|--|------------------------------------|-----|---|---|-------|-------|---------|-----|--------|---|
| | | | | Time after end of training or last test | | | | | | |
| | + - E | | | 5 days | | | 10 days | | | |
| | | | | + - E | + - E | + - E | | | | |
| Group A. Animals trained to a criterion of 85% correct responses before overtraining | | | | | | | | | | |
| C158B | 10 | 0 | 0 | 10 | 4 | 4 | . | . | . | . |
| D11B | 10 | 0 | 0 | 8 | 2 | 4 | 1 | 0 | 9 | . |
| D16B | 10 | 1 | 1 | 10 | 3 | 3 | 10 | 2 | 2 | For subsequent tests see Table 3 |
| D19B | 10 | 0 | 0 | 10 | 2 | 2 | 10 | 1 | 1 | . |
| D26B | 10 | 1 | 1 | 10 | 5 | 5 | 9 | 3 | 4 | . |
| D33B | 10 | 0 | 0 | 10 | 1 | 1 | 10 | 10 | 10 | For details see Fig. 1 |
| Mean errors | . | . | . | . | . | . | 8 | 2 | 4* | . |
| | | 1.4 | | | 3.2 | | | 5.4 | (4.0)* | . |
| Group B. Animals trained to a criterion of 75% correct responses before overtraining | | | | | | | | | | |
| C2B | 10 | 0 | 0 | . | . | . | 8 | 3 | 5 | . |
| C4B | 6 | 0 | 4 | . | . | . | 10 | 10 | 10 | For details of training see Wells & Wells (1957a) |
| C6NOL | 9 | 2 | 3 | . | . | . | 10 | 5 | 5 | . |
| C19NOL | 9 | 1 | 2 | . | . | . | 10 | 7 | 7 | . |
| Mean errors | . | . | . | . | . | . | 3 | 0 | 7* | . |
| | | 2.3 | | | | | | 6.8 | (5.8)* | . |

* Tests 6 hr. later in which 6 V. a.c. electric shocks were given after each of the first eight (D33B) or ten (C4B, C19NOL) objects presented regardless of reaction or whether the objects were + or -. Averages in brackets are calculated using scores from these retests. Where both 5- and 10-day retention tests were made, the 5-day always preceded the 10-day.

These possible masking effects must be taken into account if meaningful comparisons are to be made between the performances of individual octopuses in retention tests. In particular, it must be borne in mind that an animal taking all of the positive objects and a high proportion of the negatives is unlikely to be separating the objects with the maximum accuracy of which it is potentially capable. In

Table 1, for example, the score of D26B in its 10-day retention test (took 9 positives and 3 negatives, errors 4) is probably a reliable index of this animal's ability to separate the test objects at that time, whereas the score of D33B at 10 days (took everything) is manifestly not (see Fig. 1). When the results given in Table 1 are considered in this way it is evident that the retention test results obtained with C4B and D33B after shocks are fairer assessments of the persistence of discriminative memories than the figures obtained in the immediately preceding straightforward retention tests.

Table 1 therefore shows that although fading of discriminative memories has undoubtedly occurred during the 10 (group B) or 15 (group A) days since the end of training, in no case have the memories altogether disappeared, and that most individuals remain capable of discriminating between the objects with an accuracy of better than 75% (15 correct out of every 20 responses) for at least this long.

(2) *Experiments made with animals after vertical lobe removal*

Table 2 shows the results of exactly similar retention tests made with 18 animals having brain lesions that in most cases included total removal of the vertical lobe. Eleven of these animals averaged 4.7 errors (4.1 when a retest with C144NVB is taken into account) in retention tests carried out 5 days after the end of their training, and six of these averaged 5.4 errors after a further 10 days. In the last 20 trials of their reward and punishment training the same eleven animals averaged 2.8 errors. A second group of seven animals pretrained to a criterion of only 75% correct responses averaged 7.4 errors in tests 10 days after the end of their training (or 6.9 errors using retests), compared with 2.9 errors in the last 20 training trials.

These results are clearly similar to those reported in Table 1, considerable traces of discriminatory memories remaining apparent 10 days after the end of training. As with controls discriminatory memories can generally be revealed in animals initially taking a high proportion of both objects by subjecting the animals to repeated retention tests or to small electric shocks which reduce the tendency to react positively (Tables 2 and 3). In both cases positive responses to the negative object are eliminated before positive responses to the positive so that there is typically a transient improvement in performance as tests are continued (see also Table 4).

(3) *Length of memory retention in Octopus*

In the present investigation no systematic attempt has been made to find out how long memories of learned discriminations persist in the nervous system of *Octopus*, but in several instances retention test series were continued intermittently for a considerable time after cessation of training without entirely eliminating the tendency to react differentially towards the two test objects. Thus D11B made 8 errors in a group of 20 trials 20 days after the last test shown in Table 1—a total of 35 days from the end of training; B164NVB made only 5 errors in a retention test after the same total length of retention time (see Table 3). B161NVNSFB and C41NVB made only 4 and 6 errors respectively at 27 days, while B16B and C45NVB made 6 and 8 errors 24 and 26 days after the end of training. It should be

Table 2. Retention tests with animals having brain lesions trained to discriminate between P₁ and P₄

(Each test consisted of 20 trials, 10+, 10-. Columns show the number of times that each object was taken and total errors (column E).)

| Animal and proportion of the vertical lobe removed | In the final 20 trials of training | | | In retention tests | | | | | | |
|---|------------------------------------|---|---|---|-------|-------|--------------|---|----|---|
| | | | | Time after end of training or last test | | | | | | |
| | + - E | | | 5 days | | | 10 days | | | |
| | | | | + - E | + - E | + - E | | | | |
| Group A. Animals trained to a criterion of 85 % correct responses before overtraining | | | | | | | | | | |
| C36 NVNSFB (100%) | 10 | 2 | 2 | 9 | 1 | 2 | 4 | 2 | 8 | } 10 days later 0, 0, 10
For later tests see Table 3 |
| C37 NVNSFB (100%) | 2 | 0 | 8 | 10 | 3 | 3 | 9 | 1 | 2 | |
| C41 NVNSFB (100%) | 9 | 0 | 1 | 10 | 2 | 2 | 10 | 1 | 1 | |
| C45 NVNSFB (100%) | 7 | 0 | 3 | 9 | 3 | 4 | . | . | . | } 20 days later 7, 5, 8 |
| C49 NVNSFB (100%) | 5 | 0 | 5 | 2 | 0 | 8 | 3 | 0 | 7 | |
| C51 NVB (100%) | 10 | 2 | 2 | 8 | 1 | 3 | 4 | 0 | 6 | . |
| C144 NVB (85%) | 10 | 1 | 1 | 10 | 8 | 8 | 2 | 0 | 8 | . |
| C173 NVNSFB (100%)† | . | . | . | 10 | 1 | 1* | . | . | . | } For later tests see Table 3 |
| C188 NVNSFB (100%)† | 10 | 1 | 1 | 10 | 4 | 4 | . | . | . | |
| C189 NVB (70%)† | 10 | 2 | 2 | 10 | 4 | 4 | . | . | . | |
| C196 NVNSFB (100%) | 7 | 2 | 5 | 10 | 10 | 10 | . | . | . | . |
| Mean errors | 10 | 1 | 1 | 8 | 2 | 4 | . | . | . | . |
| | 2.8 | | | 4.7
(4.1) | | | 5.4 | | | . |
| Group B. Animals trained to a criterion of 75 % correct responses before overtraining | | | | | | | | | | |
| B158 NVNSFNOL (100%)‡ | 10 | 2 | 2 | . | . | . | 1 | 1 | 10 | } Extract from a series of tests given in full in Table 3 |
| B161 NVNSFB (100%)‡ | 9 | 1 | 2 | 9 | 4 | 5 | 10 | 7 | 7 | |
| B164 NVB (90%)‡ | 10 | 5 | 5 | 10 | 1 | 1 | 10 | 1 | 1 | |
| C9 NVNSFB (100%)‡ | 10 | 3 | 3 | . | . | . | 6 | 2 | 6 | |
| C10 NVNSFB (100%)‡ | 10 | 2 | 2 | . | . | . | 10 | 9 | 9 | |
| | . | . | . | . | . | . | 8 | 3 | 2§ | |
| C11 NVB (100%)‡ | 10 | 3 | 3 | . | . | . | 10 | 9 | 9 | . |
| C16 NVNSFB (100%)‡ | 8 | 1 | 3 | . | . | . | 8 | 6 | 8§ | . |
| Mean errors | 2.9 | | | 3.0 | | | 7.4
(6.9) | | | . |

* Second set of tests on the same day, no shocks.

† Details of pretraining given in Wells & Wells (1958). Where both 5- and 10-day retention tests were made the 5-day always preceded the 10-day test.

‡ Details of pretraining and of lesions given in Wells & Wells (1957a).

§ Tests 6 hr. later in which 6 V. a.c. electric shocks were given after each of the first 10 objects to be presented, whether + or -. Averages in brackets are calculated using scores from these retests.

remembered that all these animals had been subjected to retention tests since the end of training and that the effect of these tests, involving frequent repetition of unrewarded actions, is to eliminate responses to the test objects (Wells & Wells, 1957b). The survival of distinct responses to the test objects, despite this treatment, surely indicates that memories normally persist for considerably longer, perhaps for a period of months. Sutherland (1957) reports a retention experiment in which six animals trained to distinguish between vertical and horizontal rectangles by sight showed no decline in performance when tested 27 days after the end of

Table 3. *The proportion of acceptances, first of negative and then of positive objects, is successively reduced by repeated retention tests*

(The sequence of tests reads down the columns, which show the number of times that each object was taken and the total errors made (column E) in each group of 20 trials. Tests on the same day (bracketed together) were 6 hr. apart, otherwise overnight intervals of approximately 18 hr. except where specified. The initial interval in each case is the time since the end of training. Figures in parentheses give the proportion of vertical lobe removed. Controls and animals in column A were trained to a criterion of 85 % and those in column B to 75 % correct responses before overtraining.)

| Controls | | | Animals with brain lesions | | | | | | | |
|----------------------------|----------------------------------|-----------------------|----------------------------|--|-----------------------|-------------------------|---------|-----------------------|---------|-----|
| | | | A | | | B | | | | |
| | + | - E | | + | - E | | + | - E | | |
| D16B | 5 days | | C41 NVNSFB
(100%) | 5 days | | B158 NVNSFNOL
(100%) | 5 days | | | |
| | 10 | 3 3 | | 10 | 2 2 | | 4 | 0 6 | | |
| | 10 days | | | 10 days | | | 4 | 1 7 | | |
| | { | 10 2 2 | | { | 10 1 1 | | 3 | 0 7 | | |
| | { | 10 2 2 | | { | 10 1 1 | | 10 days | | | |
| | { | 10 0 0 | | { | 10 10 10 | | 1 | 1 10 | | |
| | { | 10 1 1 | | { | 10 8 8 | | | | | |
| | 10 shocks 20 min.
before test | 10 0 0 | | Shocks after first
10 presenta-
tions
With all 20 | { | | 10 2 2 | B161 NVNSFB
(100%) | 5 days | |
| | 10 shocks 10 min.
before test | 8 0 2 | | | { | | 10 6 6 | | 9 | 4 5 |
| | { | 10 0 0 | | | { | | 10 4 4 | | 10 | 5 5 |
| | { | 9 0 1 | | | { | | 8 2 4 | | 10 | 4 4 |
| | { | 3 0 7 | | | { | | 3 0 7 | | 11 days | |
| | { | 4 0 6 | | | C173 NVNSFB
(100%) | | 5 days | | 10 | 7 7 |
| | { | 5 0 5 | | | { | | 8 2 4 | | 11 days | |
| | { | 5 0 5 | | | { | | 3 0 7 | | 8 | 2 4 |
| { | 2 1 9 | C188 NVNSFB
(100%) | 5 days | | | | | | | |
| Fed 30 min.
before test | 3 0 7 | { | 10 4 4 | | B164 NVB (90%) | 2 days | | | | |
| { | 4 0 6 | { | 10 3 3 | | | 10 | 1 1 | | | |
| 5 days | | { | 10 0 0 | | | 5 days | | | | |
| 10 days | | { | 9 1 2 | | | 10 1 1 | | | | |
| | | { | 1 0 9 | | | 6 days | | | | |
| | | C189 NBV
(70%) | 5 days | | | 10 | 0 0 | | | |
| | | { | 10 10 10 | 10 | | 5 5 | | | | |
| | | { | 10 10 10 | 10 | | 0 0 | | | | |
| | | { | 10 10 10 | 11 days | | | | | | |
| Fed 45 min.
before test | 2 0 8 | { | 10 10 10 | 10 | | 1 1 | | | | |
| | | { | 2 0 8 | 11 days | | | | | | |
| See Fig. 1 | | C196 NVNSFB
(100%) | 5 days | 10 | | 5 5 | | | | |
| | | { | 8 2 4 | | | | | | | |
| | | { | 9 4 5 | | | | | | | |
| | | { | 3 0 7 | | | | | | | |
| | | { | 5 1 6 | | | | | | | |
| | | { | 0 0 10 | | | | | | | |

training; these animals had, however, been trained in the meantime to distinguish between the same two rectangles in oblique positions. There are no other records of experiments made to test visual retention by *Octopus* over comparable periods.

Table 4. *Animals subjected to retention tests after operations following training to discriminate between P8 and P4*

(Training was at a rate of 8 trials per day (4+, 4-) for 6 days. Retention tests were made at the normal rate of 40 trials per day, in groups of 20. Conventions as Table 3.)

| Control (dummy operation only) | | | Animals with brain lesions | | | | | |
|--------------------------------|----------|-----|----------------------------|-------------------------|-----------|-------------------------------|----------|-----|
| | + | - E | | + | - E | | + | - E |
| D ₉ B | 36 hr. | | D ₁ NVB (80%) | 36 hr. | | D ₂ NVNSFB (100%)* | 36 hr. | |
| | { 10 0 0 | | | { 10 6 6 | | | { 10 9 9 | |
| | { 10 0 0 | | | { 9 1 2 | | | { 5 4 9 | |
| | { 9 0 1 | | | { 1 0 9 | | | { 4 2 8 | |
| | { 6 0 4 | | | { 5 0 5 | | | { 2 1 9 | |
| | | | | { 3 3 10 | | | { 1 0 9 | |
| | 5 days | | | 5 days | | | | |
| | { 7 0 3 | | | { 5 10 15 | | D ₈ NVNSFB (100%) | 36 hr. | |
| | { 4 0 6 | | | { 1 7 16 | | | { 8 2 4 | |
| Fed 30 min. before test | { 0 0 10 | | D ₄ NVB (90%) | 36 hr. | | | { 7 1 4 | |
| | { 1 0 9 | | | { 10 3 3 | | { 10 1 1 | | |
| | | | { 9 1 2 | | { 10 0 0 | | | |
| | | | { 5 0 5 | | { 8 0 2 | | | |
| | | | { 2 0 8 | | 5 days | | | |
| | | | { 1 0 9 | | { 10 1 1 | | | |
| | | | 5 days | | { 10 0 0 | | | |
| | | | { 2 1 9 | | { 7 1 4 | | | |
| | | | { 0 1 11 | | { 2 0 8 | | | |
| | | | | Fed 30 min. before test | { 9 0 1 | | | |
| | | | | Fed 60 min. before test | { 6 0 4 | | | |
| | | | | | { -10 0 0 | | | |

* In this animal the superior frontal lobe was entirely removed. This disconnects the vertical lobe from its tactile input (Boycott & Young, 1955) so that for purposes of comparison this animal may be regarded as having the vertical lobe entirely removed, although a part of the extreme right hand gyrus of this lobe (about 15% of the total volume of the lobe) remained intact after the operation.

DISCUSSION

The object of the present series of experiments is to establish whether or not memories of things touched fade more rapidly in animals from which the vertical lobe of the brain has been removed. The records of retention tests with 'no vertical' and control animals clearly show that there are no gross differences in the performances of the two groups of animals. Both are subject to the same tendency to revert to positive responses in the absence of tests, and both can be shown to retain effective discriminatory memories for at least 10 days after cessation of training.

The performance of control and 'no vertical' animals is compared in greater detail in Table 5. It is apparent from this that the system of training animals to

Table 5. *Summary of results of retention tests*

| | In final 20 trials of training | In retention tests | |
|--|--------------------------------|---|--------------|
| | | Time after end of training or last test | |
| | | 5 days | 10 days |
| <i>(a) Mean errors per 20 trials</i> | | | |
| Groups A. Animals trained to a criterion of 85 % correct responses before overtraining | | | |
| Controls | 1.4 | 3.2 | 5.2
(4.0) |
| Animals with vertical lobe lesions | 2.8 | 4.7
(4.1) | 5.4 |
| Groups B. Animals trained to a criterion of 75 % correct responses before overtraining | | | |
| Controls | 2.3 | . | 6.8
(5.8) |
| Animals with vertical lobe lesions | 2.9 | . | 7.4
(6.6) |
| <i>(b) Increase in errors per 20 trials</i> | | | |
| Groups A. Animals trained to a criterion of 85 % correct responses before overtraining | | | |
| Controls | . | 1.8 | 3.8
(2.6) |
| Animals with Vertical lobe lesions | . | 1.9
(1.3) | 2.6 |
| Groups B. Animals trained to a criterion of 75 % correct responses before overtraining | | | |
| Controls | . | . | 4.5
(3.5) |
| Animals with vertical lobe lesions | . | . | 4.5
(3.7) |

(Figures in parentheses are calculated using scores made in retests (see p. 339).)

a prescribed criterion of accuracy regardless of the length of training required has failed to achieve its object of ensuring the same standard of accuracy of response in control and 'no vertical' animals before retention tests. All of the animals attained the prescribed criterion (85 or 75 % correct responses in a group of 20 trials), although those lacking the vertical lobe were slower to do this (Wells & Wells, 1957*a*), but improvement thereafter during overtraining was greater in controls than in the octopuses lacking vertical lobes. It had been hoped to avoid this by overtraining each individual for a number of trials equal to that needed to reach the prescribed criterion, but the attempt was unsuccessful, and one must conclude that the presence of the vertical lobe becomes relatively more important in the later phases of learning when the accuracy of a response is in the process of refinement towards the optimum of which the animal is capable. This finding is consistent with what we know about the relatively greater effect of vertical lobe removal upon the performance of octopuses in difficult discriminations (Wells & Wells, 1957*a*; Boycott & Young, 1957).

So far as the present series of tests is concerned this finding means that animals lacking the vertical lobe begin their retention tests with memories rather less well established than their controls. The process of forgetting in the two preparations must be studied relative to their respective starting-points. In the case of group A controls, for example, the 10-day retention test figure of 5.2 errors (4.0 when retests are considered) must be compared with a starting accuracy of 1.4 errors per 20 trials, and the 5.4 of the 'no verticals' with 2.8. This has been done in Table 5*b*, which shows the increase in number of errors made per 20 trials in successive retention tests; almost exactly similar figures are obtained from experiments with controls and 'no vertical' animals. In view of the wide range of individual scores made in these tests and the rather small number of animals involved (28 in all) it would be unwise to pretend that the experiments summarized in Table 5 show conclusively that memories fade at the same rate in animals with and without vertical lobes. The results do, however, suggest very strongly that this may be the case, and in any event give no grounds for supposing that any considerable difference in the rate of memory fading is produced by vertical lobe removal.

These results are consistent with the hypothesis that at least in so far as touch is concerned the vertical lobe plays a part in the establishment of memories during the time that the sensory stimuli concerned are being received but not in the maintenance of these memories between trials. Its removal renders each sensory experience less effective in the establishment of memories, but does not affect the rate at which whatever changes have occurred in the nervous system fade away between such events (Wells & Wells, 1957*b*).

SUMMARY

1. Octopuses were trained to make a tactile discrimination until they attained a criterion of either 75% or 85% correct responses in twenty successive trials. They were then overtrained for an equal number of trials. Retention of training was tested in twenty unrewarded trials with the same objects 5 or 10 days later.
2. Exactly similar experiments were made with animals trained after removal of the vertical lobes of their brains; these animals were slower to learn, but once trained to a similar standard of accuracy of response they forgot their training at the same rate as controls.
3. This shows that while the presence of the vertical lobe enhances the effect of experience on the establishment of memories causing discrimination of things touched, it does not affect the maintenance of these memories once established.

The experiments listed in this account were made during the period 1955-6, while M.J.W. was holding an Eli Lilly Fellowship as a member of the staff of the Stazione Zoologica in Naples, and during a visit to the Stazione in the summer of 1957, while holding a Fellowship at Trinity College, Cambridge. The authors would like to thank the Director and Staff of the Stazione for their hospitality to an ex-colleague and to thank Prof. J. Z. Young F.R.S., and Mr B. B. Boycott for reading and criticizing this work in manuscript.

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