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RATES OF ESTABLISHMENT OF REPRESENTATIONS IN THE MEMORY OF OCTOPUSES WITH AND WITHOUT VERTICAL LOBES

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INTRODUCTION

Numerous experiments have shown the capacity of *Octopus* to learn to attack one figure and avoid another, but there has been no thorough study of the rate of learning under various conditions, such as the spacing of trials and the method by which the reward is given to the animals. In the present experiments a systematic investigation was made of the setting up in the memory of representations that promote or prevent attack, in sets of animals under controlled conditions. It thus becomes possible to compare the rate at which the representations are established in normal animals and in those lacking the vertical lobes. 'Memory' is here used to denote the neural network within which sets of connexions are established when certain sets of attributes recur in combination with stimuli such as food or pain that evoke specific responses. Such sets of connexions are then referred to as representations ensuring the appropriate responses (Young, 1959, 1960*a*).

The experiments were designed to answer the following questions:

A. Are representations ensuring attack at a figure set up only if food is given at the place where the figure is shown, or can they be established by showing the figure in one place and feeding in another?

B. At what rate are such representations set up with trials (*a*) at long intervals, and (*b*) at short intervals?

C. What are the rates of their formation after removal of the vertical lobes?

D. How does removal of the vertical lobes influence the time for which the effects of a shock in preventing attack can be detected?

METHODS

Octopuses were isolatedi n rectangular tanks with opaque sides and lids. They were given bricks as a home at one end. The figures were opaque white plastic rectangles shown moving up and down on a transparent rod, inserted through an opening in the lid at the end of the tank away from the home. The times between inserting the rectangle and completion of the attack were taken with a stop-watch.

Operations for removal of the vertical lobe and assessment of the amount removed were as described by Boycott & Young (1955*a*).

EFFECT OF POSITION IN WHICH FOOD IS GIVEN

Eighteen octopuses were isolated and tested for 3 days twice daily by showing crabs but not allowing these to be eaten. Attacks were made at about 8/10 trials. No food was given on these days. The animals were then divided into three sets. All were shown a white vertical rectangle 1 m. from the home, at 10 min. intervals, ten times daily, at morning and evening sessions (Fig. 1). The animals of set A were given

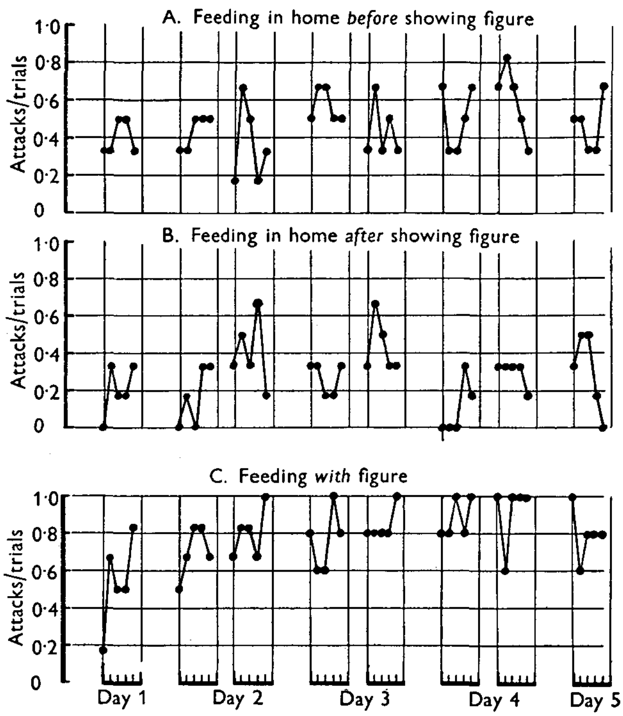

Fig. 1. Effect of place and time of reward on learning to attack a white vertical rectangle. Five normal octopuses in each group. Each point shows the proportion of animals that attacked when the rectangle appeared. See text. Only the animals in set C, where the reward was given close to the figure, learned to come out to attack.

a small piece of fish in the home immediately before showing the rectangle, the fish being introduced on the end of a wire. In set B the rectangle was shown until it was attacked, or for 20 sec., and food was then given to the octopus in its home, the rectangle being first pulled away if there had been an attack. The third set, C, were fed when there was an attack, or after 20 sec., the food being put near to the rectangle, so that the octopus seized both together. If there was no attack, even when the fish was put in, then fish and rectangle were moved towards the home until an attack occurred.

At the first trial of the first session the animals in groups B and C showed almost no attacks, no representations ensuring attack at this figure being present. In group A there were some attacks, due to the stimulus of feeding (Young, 1958). At subsequent trials of the session there were more attacks in all three groups, but the effect was markedly greater in group C, where the food was given with the figure (Fig. 1). By the end of the first session of five trials the animals in this group were attacking 8/10 times. On this first day there was only one session.

The next morning there were no attacks by group B at the first trial, they had learned nothing from the day before. Group C, on the other hand, attacked at half the trials. In group A there were the same number of attacks as at the first trial of the first day. Group C was, therefore, the only one to show signs of an increased tendency to attack. Moreover, the mean time taken to attack began to fall steeply in these animals that were fed with the figure (Fig. 3).

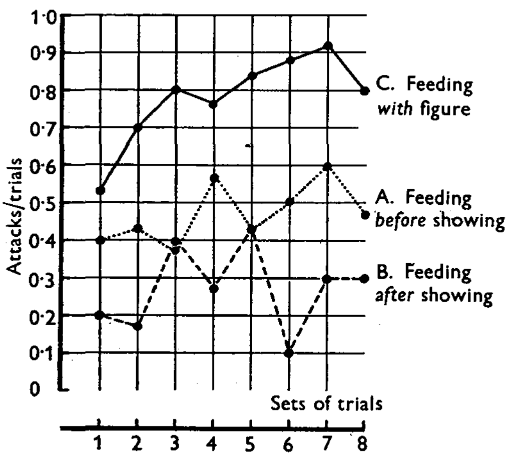

Fig. 2

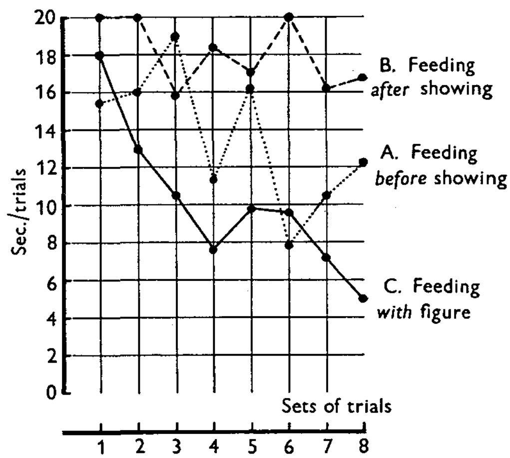

Fig. 3

Fig. 2. Mean proportion of attacks at each session of the experiment in Fig. 1.

Fig. 3. Mean delay before attack at the first trial of each session of Fig. 1. When there was no attack the time was taken as 20 sec.

This pattern of behaviour continued throughout the 5 days of the experiment. The animals in group C, where food was given with the rectangle, showed an increasing proportion of attacks at the first trial of each successive session, until finally attacks were made on the great majority of occasions (Figs. 1, 2). The mean time taken to make the first attack of the session fell from 18 sec. at the trial of the first session to 5 sec. at the eighth session (Fig. 3). The animals fed in the home after showing the figure (Group B) gave an irregular performance, with a slight tendency to increased numbers of attacks both at the first trial of each set and in the means for each set. There was no decrease in the times taken to attack. There was, therefore, at most a slight formation of representations promoting attack; after 5 days attacks still occurred only on 3/10 occasions.

The animals in group A showed rather more attacks than those in B, as is to be expected since the rectangle was always shown during the period of raised excitability after feeding. However, the increase in proportion of attacks is about the same as in group B and far less than in group C. After 5 days, attacks were still only made on half the occasions. The times to attack at the first trials of each session were irregular and fell only from 15 to 12 sec.

This result was confirmed in another series of sixteen animals. For 5 days these were given food in the home, half of them before and half after showing a horizontal rectangle. At the beginning of the experiment both groups attacked only on 1–2/10 occasions. At the beginning of the fifth day those fed after showing attacked on 1/10, those fed before not at all. In neither group had representations ensuring attack been set up in the memory.

On the sixth day both groups were fed *with* the figure on three occasions. The number of attacks rapidly increased and on a fourth trial at the end of the day there were 9/10 attacks. The next morning there were attacks at about half the trials.

We may conclude that for the setting up of representations that promote attack at visible figures it is important that the food should be presented close to the figure, so that the two are seized together. Food given in the home before or just after the attack does not ensure the formation of such a representation in the memory.

SETTING UP OF REPRESENTATIONS PROMOTING ATTACKS, WITH TRIALS AT LONG AND SHORT INTERVALS

Twenty animals were isolated for 4 days and then operated, half for removal of the vertical lobe and half with a dummy operation. After allowing 2 days for recovery all were trained to attack a white vertical rectangle, half of each sort with trials at 5 min. intervals, the other half at 50 min. intervals. Food was given as soon as each animal attacked. If there was no attack within 15 sec. a piece of fish was placed near to the rectangle and the two were moved towards the octopus until the food was taken. There were eight trials each day, given at morning and evening sessions. Considering here the normal (dummy-operated) animals we see that there was an increase in frequency of attacks and decrease in their delay in both 5 min. and 50 min. groups (Fig. 4). The only consistent difference between the groups was that improvement in performance went on rather longer with the 5 min. trials, producing slightly higher criteria at the asymptote. There were consistent differences in behaviour between individuals, some learning more quickly to come out with a short delay. However, the pattern was the same for all. At the beginning none came out regularly and all showed long delays. By the end nearly all were very regular and the delays were much less. On some occasions all five animals in a set attacked with a delay of only 2 sec., which is the minimum that can be reliably recorded with this method.

EFFECTS OF VERTICAL LOBE REMOVAL ON SETTING UP OF REPRESENTATIONS PROMOTING ATTACKS

The animals without vertical lobes in the series in Fig. 4 showed no consistent increase in number of attacks or reduction in their time with training either at 5 min. or 50 min. intervals. This confirms previous evidence that representations ensuring

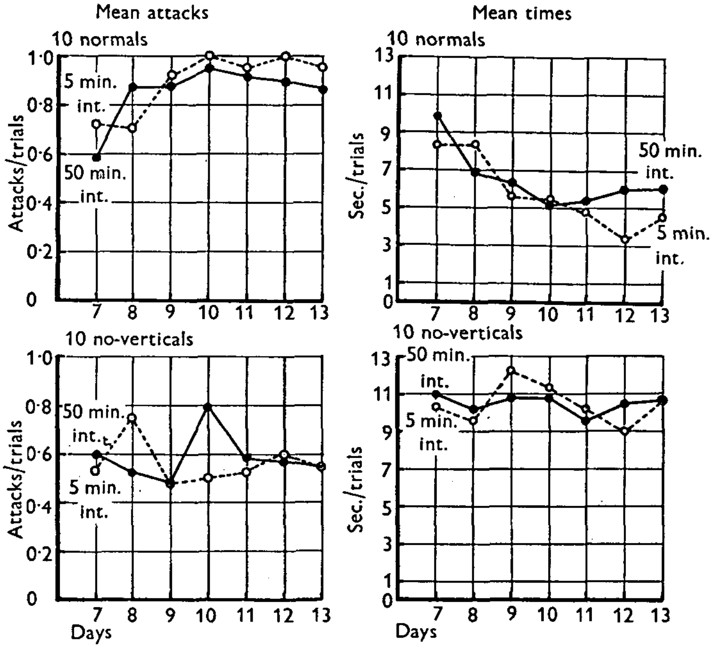

Fig. 4. Effect of interval between trials on learning to attack a white vertical rectangle. Open circles, trials at 5 min. intervals; filled circles, trials at 50 min. intervals. The points show the means for the ten trials each day. Above, ten normal animals; below ten with vertical lobes removed (94 %). Series KBA.

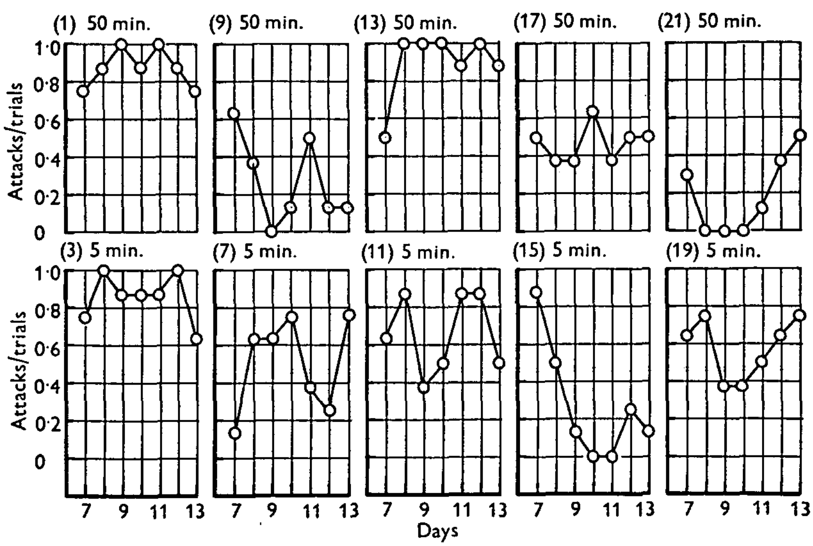

Fig. 5. Mean attacks per day by each of the individual operated animals of Fig. 4. The figures in brackets are the serial numbers of the animals.

attacks are set up in the memory only with difficulty after this operation (Young, 1960*a*). There were considerable differences between individuals in the tendency to attack (Fig. 5). Three attacked consistently throughout and the others fluctuated, all attacking sometimes, but none with steadily increasing frequency. There was no obvious pattern to the distribution of these attacks. An individual would show no attacks during the four morning trials and then come out at every trial in the afternoon. Then later its attacks would be quite scattered among the trials.

Injury to the lobes below the vertical lobe may affect the tendency to attack. None of these animals had serious lesions in these regions. The subvertical lobes were somewhat damaged in octopus 3, but this was one of the most persistent attackers. In all of them more than 90 % of the vertical lobe had been removed (mean 94 %).

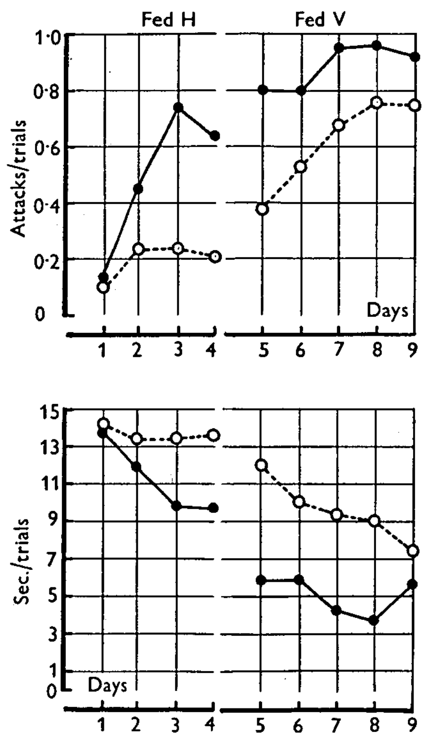

Fig. 6. Learning to attack horizontal and vertical rectangles by five normal animals (filled circles) and eleven without vertical lobes (open circles). 88 % had been removed. The points show the proportion of attacks made and the mean times during the five trials of each day, given at 15 min. intervals. Learning is much slower by the operated animals. Series JYA.

A similar result was seen in a further series of five normal and eleven no-vertical animals (Figs. 6, 7). On the day after operation (day 1) both groups tested with a white vertical or horizontal rectangle attacked either of these at about 1/10 occasions. For the next 3 days they were given five trials a day at which the horizontal rectangle was shown, and fish was given if attacks were made, or after 15 sec. if there was no attack. The fish was given with the figure and the two were pushed towards the octopus if necessary. Trials were at approximately 15 min. intervals. The normal animals rapidly learned to attack the rectangle on about 7/10 occasions, though always with rather long delay. The animals without vertical lobes showed hardly any increase in proportion of attacks.

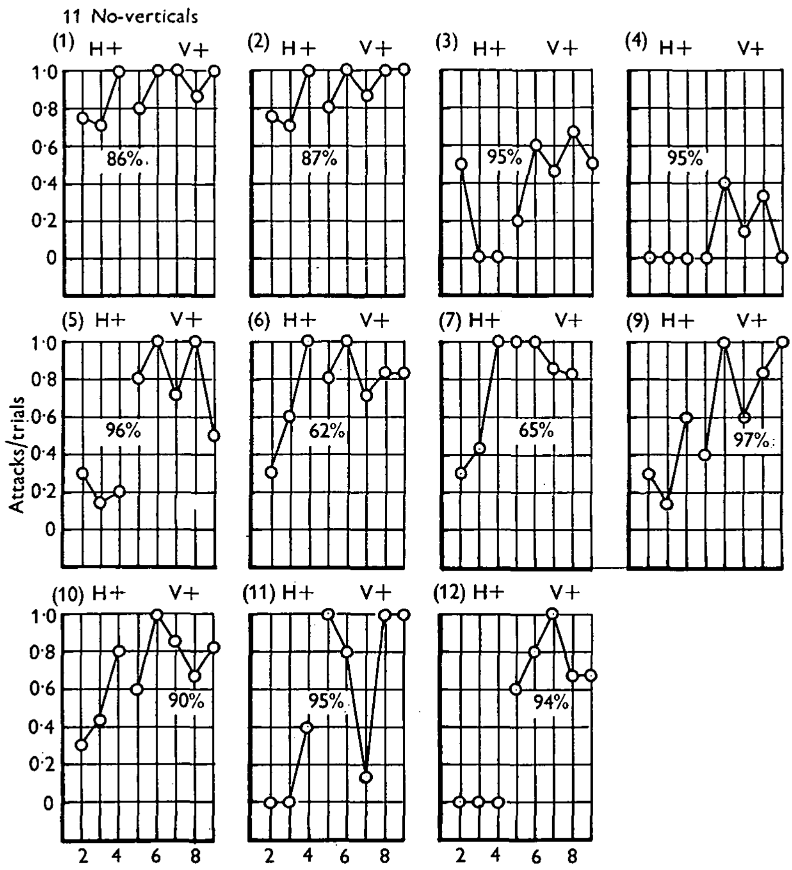

Fig. 7. Behaviour of the individual operated animals of the experiment of Fig. 6. The figures in brackets are the serial numbers of the animals.

Then from the 5th to 9th days similar tests were continued with a vertical rectangle. The normal animals attacked this about 8/10 times at first and soon came to do so almost always and with short delay. The no-verticals at first attacked about 4/10 times and then some of them gradually learned to do so, until the mean was nearly 8/10 times and the delay shorter (Figs. 6, 7). As before there were considerable and consistent differences between individuals. Two were persistent attackers throughout (numbers 1 and 2). Five became fairly persistent and two others attacked frequently but irregularly (numbers 5 and 11). Two attacked at less than half the trials (numbers 3 and 4). There was no serious injury to the underlying lobes to connect with the tendency to attack. A mean of 88 % of the vertical lobes had been removed, with extremes of 62 and 97 %. There is no obvious correlation between the number of attacks and the amount of tissue remaining. The rate at which the representations were established in the memory was obviously much less than in the normal animals. No exact comparison of rates can be made, but after five occasions of feeding with the vertical rectangle the normal animals were attacking more reliably and with shorter delays than the no-verticals after twenty-five trials. By this criterion the memory system is at least five times less efficient after vertical lobe removal.

SETTING UP OF REPRESENTATIONS PREVENTING ATTACKS AT A RECTANGLE

The effect of shock in reducing the tendency to attack a previously 'positive' figure was tested in the series described in the last section by giving on the morning of each of the next 4 days three shocks following showings of the white vertical rectangle. On the first day every animal was shocked at each of the three trials, whether or not an attack had been made, the electrodes being introduced into the home if necessary. Thereafter no further shocks were given to the normal animals; the no-verticals were shocked only if they attacked.

In order to test the persistence of the effect of the shocks tests were then made 15, 30, 60 min, 2 and 4 hr. after the shocks on each day (Figs. 8, 9). As control, six of the no-vertical and two of the normal animals were tested throughout by showing the rectangle but not given any shocks. We thus distinguish between an 'extinction group' (the controls) and a 'shock group'. All the animals were fed with fishes each evening, some hours after the tests.

The normal animals, after they had been shocked three times, stopped attacking and made very few further attacks throughout the 4 days. The 'extinction group' of normals continued to attack in spite of the absence of rewards, though not at every trial. The animals without vertical lobes, after the first three shocks, stopped attacking but then mostly began again by the end of that day. Although the representations ensuring attack had been 'weaker' than those of the normal animals the tendency to attack was less affected by the shocks, because the process of setting up representations *preventing* attack was also weak. On the next (eleventh) day, however, fewer came out and on the 12th and 13th days attacks became still further depressed so that at the end none was attacking. Tests with crabs, however, then showed attack by nearly all the animals.

The control group of animals without vertical lobes, tested without shock, also showed some falling off in attack each day as a result of extinction, which has been shown to occur readily in octopuses without vertical lobes when the representation ensuring attack is 'weak' (Young, 1959).

However, these control animals recovered after extinction to a full level of 100 % attacks on each subsequent morning. The difference between the 'shock' and 'extinction' groups at the beginning of each day thus shows signs that there is some cumulative effect, even in these operated animals, of the shocks in setting up representations that prevent attacks. This process, was however, very much slower than in the normal animals, which after the shocks on the first day showed only rare attacks during the subsequent days. Exact comparison is difficult, but three shocks were sufficient to prevent attacks almost completely by the normals for 24 hr. and signs of the effect could be seen for much longer. In the no-verticals little or no effect of three shocks was seen 24 hr. later. Even after nine shocks many attacks were made. The process of forming representations in the memory that prevent attack is again at least five times less efficient without vertical lobes, using time of persistence as criterion.

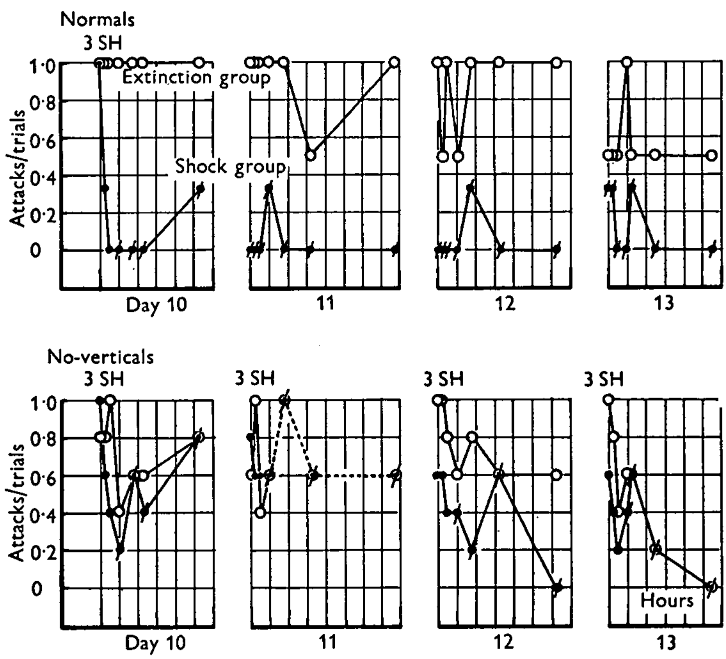

Fig. 8. Effect of shocks in preventing attacks at a 'positive' figure. The animals had all learned to attack a white vertical rectangle on days 1–9 as shown in Fig. 6. Then on day 10, three of the normals and five no-verticals were given shocks on three occasions after showing the rectangle (filled circles). Their responses were then tested by no-reward trials (crossed circles). The normal animals were given no further shocks but the operated ones received three further shocks at the beginning of each of the next 3 days. Two normal and five no-vertical animals provided control 'extinction' groups (open circles). These were shown the rectangle without reward or shock.

REPRESENTATIONS PREVENTING ATTACKS AT CRABS IN NORMAL ANIMALS AND AFTER VERTICAL LOBE REMOVAL

Normal octopuses that have received shocks following attacks at crabs soon cease to attack. The representation preventing attacks may then last for several days. In animals without vertical lobes it disappears more rapidly (Boycott & Young, 1955*b*).

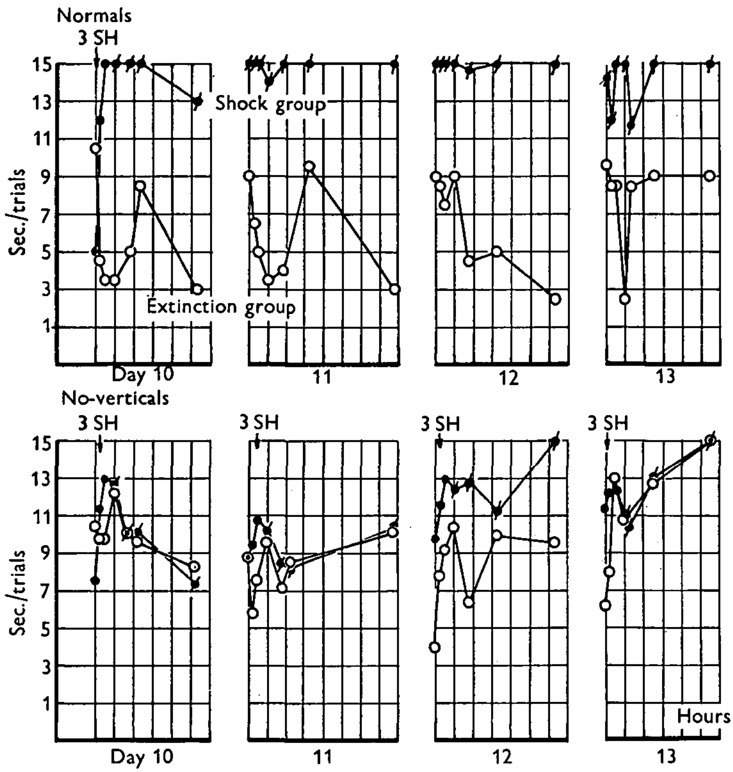

Fig. 9. Mean times to attack in the experiment of Fig. 8.

This has been confirmed in the present series by showing crabs to normal and no-vertical octopuses and giving shocks whenever there were attacks. The trials were given at 6 min. intervals, in sets of ten in the morning and ten in the evening of each day. As before, half the animals of series JYA were used as controls for the possibility of extinction, being simply tested with crabs, without reward or shock when there were attacks.

In the normal animals attacks ceased after each had received two or three shocks and were only resumed 3 days later (Figs. 10, 11). During the period when there were no attacks the white vertical rectangle was shown occasionally and was sometimes attacked. The representation preventing attack was thus at least partly specific to crabs. The normal animals that were given no shocks attacked on almost all occasions. The only signs of extinction were slight increases in delay (Fig. 11).

The animals without vertical lobes showed much greater persistence in continuing to attack crabs in spite of shocks. During each of the first ten trials at least one of the six octopuses in the 'shock' groups made an attack. No individual octopus attacked every time, each stopped and then after a few trials started again.

Seven hours later nearly all again attacked and the attacks fell off approximately as in the first set, that is, there was no clear sign of retention of the representations set up in the morning (Figs. 10, 11). However on the next day (day 15) the attacks declined much more rapidly than before, and after the fifth trial no further attacks were made. Some information had therefore survived in the memories from the previous day. No such decline appeared in the five operated animals of the 'extinction' group, which were simply shown the crabs without reward and continued to attack on nearly every occasion, although not quite so regularly as the normal octopuses.

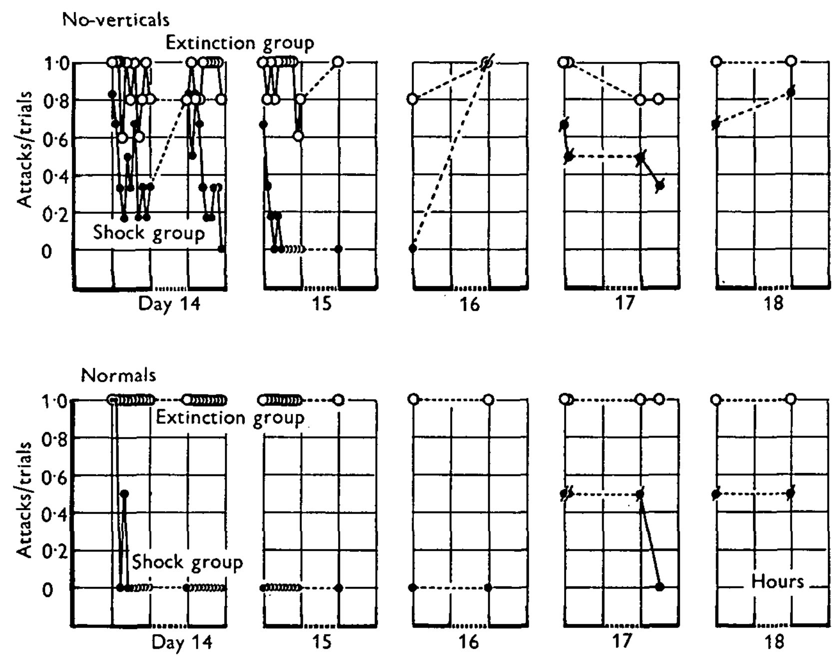

Fig. 10. Effect of shocks in preventing attacks at crabs. Continuation of experiment of Figs. 8 and 9 with division into groups to which shocks were given for every attack at crabs (filled circles) and extinction groups that were shown crabs but not allowed to eat them. After day 15 no further shocks. Trials on days 14 and 15 at 6 min intervals. On subsequent days tests in morning and evening (crossed circles).

No further shocks were given after day 15, but the animals were tested for 3 further days by showing crabs without reward, to discover the duration of the representations that prevent attack. The normal octopuses showed no attacks until the third day after the shocks and few even thereafter. The animals without vertical lobes, tested 7 and 24 hr. after shocks had last been given, showed no attacks. However, by 36 hr. many attacks were made by the shocked animals, though with longer delay than by the 'extinction' group, which had not been shocked (Fig. 9). Throughout the 3rd day after shocking, attacks were less frequent and slower by the shocked group and there were still some signs of a difference on the 4th day.

As explained on p. 50 a mean of 88% of the vertical lobes had been removed from the whole group of eleven animals, without significant injury to the underlying lobes. The individuals that had been the most regular attackers during the period of feeding with the vertical rectangle (numbers 1 and 2) were also among the animals that attacked crabs most persistently. However, even in these two the proportion of attacks became less by the 15th day.

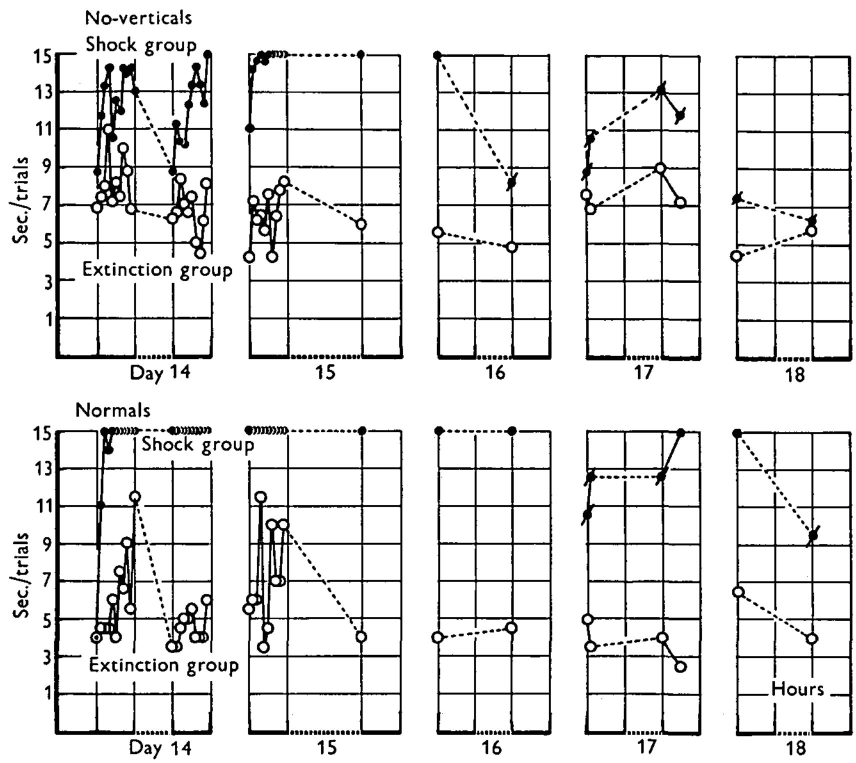

Fig. 11. Mean times to attack in the experiment of Fig. 10.

Representations preventing attack at crabs can thus be set up in the memory in the absence of the vertical lobes, but the process is much slower than in normal animals. More shocks are needed before attacks cease and, if the animals are left to forget, attacks begin again sooner in the operated animals. The no-vertical group required a mean of ten shocks before reaching a level at which no attacks were made for five trials. In the group of normal animals this level was realized after two shocks by one animal and three by the other. The memory is again at least five times more efficient in the normal animals.

Once established, the representations preventing attack remained fully effective in the operated animals for only 24 hr., though there were signs of its presence for 4 days. The data for the normal animals are inadequate, but there were clear signs of the effects of two shocks after 4 days.

EFFECT OF SHOCKS AT LONG AND SHORT INTERVALS IN PREVENTING ATTACKS IN ANIMALS WITHOUT VERTICAL LOBES

It has previously been suspected that the deficiency in learning by animals without vertical lobes lay in a failure to summate the effects of trials unless they were given close together (Boycott & Young, 1955*a*; Young, 1960*b*; Wells & Wells, 1957). Comparison was therefore made between the effects of shocks given at intervals of 6 and 60 min. The animals considered in the last section were used, some of which had already received shocks and others which had been used as controls on extinction with unrewarded tests. Two groups were now prepared; five in one and six in the other, both groups containing some that had and some that had not received shocks. Every animal was shown crabs four times and given a shock whether it attacked or not, in the latter case the shock being given in the home. For the six in group A the trials were spaced at 6 min. intervals, for the five in group B at 60 min. intervals. Thereafter all were tested by showing crabs without reward (Fig. 12).

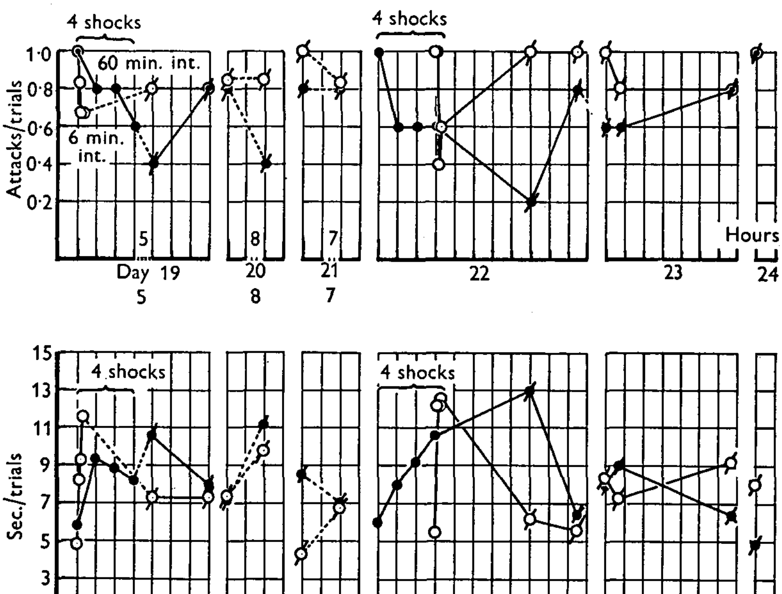

Fig. 12. Effect of shocks at 6 min. intervals (open circles) and 60 min. intervals (filled circles) in preventing attacks at crabs by animals without vertical lobes. The same octopuses as Fig. 10 but divided into two new groups. The shocks were given at the first four trials on days 19 and 22. At all the other trials crabs were shown but no reward or shock given when they were attacked (crossed circles). The effect of the shocks is more marked if they are widely spaced.

In group A there were altogether nineteen attacks out of the twenty-four occasions at which shocks were given (0·79), whereas in group B there were sixteen shocks out of twenty trials (0·80). During subsequent tests on the day of shocking those given shocks at short intervals came out considerably more often and with shorter delays than those shocked at hourly intervals (Fig. 12). The same relationship was maintained during further tests without reward or shock on the following 2 days (20 and 21). By this time in both groups the level of attacks before shocking was nearly but not quite regained.

On the 22nd day, in order to repeat the experiment, the groups were reshuffled to form two new ones, each with some animals of the previous groups A and B. The new group C was given four shocks at 6 min. and D four shocks at 60 min. intervals. As before, the proportion of attacks during the shocking period was similar (0·75 for C, 0·70 for D), but the effect again lasted longer in those shocked at long intervals (Fig. 12). The difference had disappeared by the end of the next day (day 23).

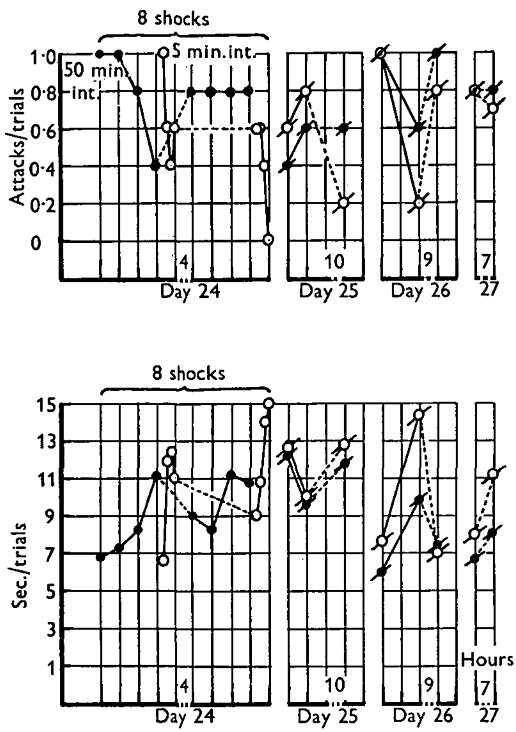

Fig. 13. Continuation from Fig. 12 with the animals re-arranged into two new groups. On day 24 eight shocks given at either 5 min. intervals (open circles) or 50 min. intervals (closed circles).

In order to repeat this experiment with a greater number of shocks the animals were again reshuffled on day 25 into groups E and F, each containing a similar number from C and D. Group E was given eight shocks at 5 min. intervals in two groups, four in the morning and four 7 hr. later. Group F was given eight shocks at 50 min. intervals, again in morning and evening groups (Fig. 13). This time the immediate depression produced by the shocks at short intervals was the greater. The animals shocked at short intervals attacked only at 0·525 of the trials as against

0·725 for the others. During the subsequent 3 days the frequency of the attacks and their delay were similar in the two groups, those receiving shocks at short intervals remaining somewhat less ready to attack.

From these experiments it is clear that there is no very marked difference between the effect of trials at long and short intervals in setting up representations that prevent attacks upon crabs. If anything a few shocks close together are less efficient than the same number separated by an hour in preventing attacks during the ensuing period. The results are summarized in Fig. 14, where the animals given shocks at long and short intervals are considered as two continuous series. By the reshuffling it was ensured that every animal had both treatments at some time during the experiment and the greater effect of the more widely spaced trials is therefore probably significant, for the condition that only a few shocks are given each day, but the differences are not great.

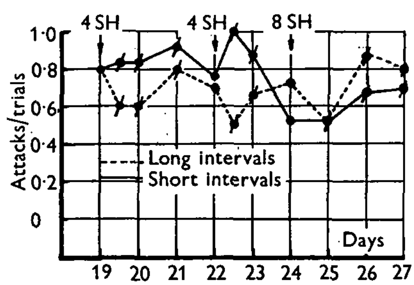

Fig. 14. Summary of the experiments of Figs. 10–13. Mean attacks on the occasions when shocks were given at different intervals and during the subsequent days. The shocks at longer intervals produced the greater effect when there were four of them. With eight there was little difference.

DISCUSSION

These experiments serve to establish some of the conditions under which representations promoting or preventing attack are set up in the memory of *Octopus*. The situation as regards learning to attack is complicated by the fact that these animals tend to come out to attack all objects more readily during the period after they have been fed. It has been established, however, that such attacks during the period of raised excitability do not result in learning to attack (Young, 1960*a*). This result is confirmed by the animals of Fig. 1 A. Figs. 1 B and C show the new point that feeding after showing is only effective if the food is given near to the figure. For survival it is reasonable that this should be so, there would be no point in learning to go out to attack if the food is to be found in the home. However, the mechanism by which this 'correct' result is secured remains obscure. It may be that there is a complicated interplay between the three sets of information provided by the object seen, touched and tasted. In the vertical lobe system impulses from these sources are brought together (see Young, 1960*b*), and this may be the means by which this lobe serves to promote the setting up of representations that ensure attack. However, as Figure 6 shows, such representations can be slowly formed in the absence of the vertical lobes. The optic lobes themselves receive tracts from the arms, both directly in the brachio-optic tract and through the inferior frontal-optic tract (Boycott & Young, 1956).

The fact that learning takes place at much the same rate with rewards spaced at 5 and 50 min. agrees with experience with other animals. Pennington & Thompson (1958) found that rats learned a vertical-horizontal discrimination fastest with trials at 3 to 4 min. intervals, but between 5 min. and 24 hr. there was little further change. There is probably no general solution to this problem and it may be that for difficult problems distributed effort is more effective, for easy ones massed effort.

Learning not to attack an object that yields shocks involves bringing visual information together with that from pain receptors. This learning also can proceed slowly in the absence of the vertical lobes. The experiment of Fig. 12 suggests that shocks close together in time may actually be less efficient than more widely spread ones in these deficient animals. It has already been shown that part at least of the defect of these operated animals is that the effects of a shock in preventing attack wear off more rapidly than in normal animals (Young, 1960*a*). These two results are not necessarily inconsistent. For long-lasting learning to occur some trace must remain even when the animals have again begun to attack. In the summation of this with the traces left by subsequent trials it may well be that time itself is required for whatever process of growth establishes the connection. Further traces provided at intervals of say 1 hr. may thus be more effective than the same number provided at 5 min. intervals. Wells & Wells (1958) have discovered evidence that representations ensuring correct tactile response in *Octopus* only become fully established after a lapse of time.

The memory system appears to be at least five times less efficient after vertical lobe removal, as judged by the number of trials required to reach a given criterion of performance. The impairment appears to be of the same extent for the setting up of representations that ensure attack at a rectangle and those that prevent attack at a rectangle or a crab. In a previous study an impairment of 3–4 times was estimated by a somewhat different method (Young, 1960*b*).

In the daily life of the animal an impairment of this order would evidently have most serious consequences both for obtaining food and avoiding enemies. An octopus cannot afford to wait for a long process of learning such as humans use and psychologists often rely on for animal experiments. Octopuses have been shown to be able to make approximately correct discriminating reference to two figures after three or four trials (Young, 1960*a*). An increase by five times would be serious.

The capacity of the vertical lobes to produce this result is out of proportion to their size. They are estimated to contain 25 million cells (mostly very small), as against 60 million in each of the optic lobes. However, the latter are presumably primarily concerned with coding the information received from the retina, and they receive few fibres from the arms or other sources. In the superior frontal and vertical lobes all the relevant information is brought together. It is partly stored in them, but also passed back to the optic lobes in a form suitable for storage.

SUMMARY

1. The rate of learning to attack a rectangle seen at a distance was studied under various conditions.

2. Learning is rapid only if the food reward is given after the figure has been shown, and if it is near to it.

3. There was no learning to attack if the food was given in the home before showing the figure, nor if the food was given after the octopus had returned to its home.

4. There was no marked difference in rate of learning with trials at intervals of 5 and 50 min.

5. After removal of the vertical lobes learning to attack a rectangle occurred only slowly. Operated animals attacked less reliably after twenty-five trials than normal animals after five trials.

6. After being shocked three times following showings of a rectangle normal animals that had previously learned to attack made few further attacks during the next 4 days. Animals without vertical lobes began to attack again during the same day; little sign of the effects of shocks was seen after 24 hr.

7. The process of forming representations that prevent attack is estimated to be at least five times less efficient in animals without vertical lobes.

8. This was confirmed by the effect of shocks in preventing attacks at crabs. In normal octopuses attacks ceased after two or three shocks at 10 min. intervals and were only resumed 3 days later. Animals without vertical lobes attacked up to ten times in spite of shocks. A few hours later all attacked again. However, some evidence of more enduring representations in the memories was seen.

9. There was no great difference in the effect of shocks given at intervals of 5 and 50 min. in preventing subsequent attacks at crabs by animals without vertical lobes. Under some conditions the more widely spaced shocks produced the greater effect.

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