# VISUAL RESPONSES BY OCTOPUS TO CRABS AND OTHER FIGURES BEFORE AND AFTER TRAINING

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## INTRODUCTION AND METHOD

Octopuses are able to learn to make distinct reactions by sight to objects of different shape (see Boycott & Young, 1956). Previous experiments have mostly been devoted to training the animals by means of shocks not to attack a figure of one shape, while continuing to attack another figure that is rewarded by giving food. In the experiments reported here each octopus was first fed for several days in its home. Then a single figure was shown at a distance at successive trials and associated either with food or shock. In this way one can study the initial responses of the animals and then watch the growth of memories that are either 'positive', that is increase the probability of attack, or 'negative', if they reduce the attacks at a particular figure. The experiments were made as before (Boycott & Young, 1956) in elongated tanks 100 × 40 × 40 cm., with bricks at one end, among which the octopus made its home. A figure shown at the opposite end of the tank was then made 'positive' by feeding with a dead fish if it was attacked; if there was no attack after 15 sec. a fish was introduced on a thread near to the figure. Alternatively, the figure could be made 'negative' by giving a shock if it was attacked, by electrodes attached to a holder introduced for the purpose and giving 6 V. a.c. An animal being trained to give a negative response in this way was given food at other times by dropping dead fishes into the end of the tank near the home. In order to maintain as far as possible a constant state of hunger this feeding was done at intervals throughout the day, between trials.

As a third possibility the figure shown was withdrawn if it was attacked, without giving either food or a shock. A standard time of 30 sec. was adopted for such tests, the figure being then withdrawn if there had been no attack.

The figures used were made of plastic sheet, either opaque black or opaque white, 3 mm. thick. They were attached to rods of transparent plastic, and were introduced into the tanks from above and moved up and down at a rate of two to three times a second throughout the trial.

Trials were given four times a day, with at least an hour between. Nothing was done to disturb the octopus between trials except for giving food as described above. The tanks were made of opaque asbestos sheeting. In the lid was a hole, which was covered with a wire grating between experiments. There was diffuse daylight or electric light above the tanks. The grating was removed several minutes before a trial and the figure introduced through the hole. The octopus could therefore not see the observer and the figure appeared in the dimly lit area beneath the hole. A few of the experiments were made in tanks with open tops, where the octopus and observer could see each other, a situation with obvious disadvantages as well as advantages. The results were similar in the two types of tank.

In many of the experiments the vertical lobe system was partly interrupted either before or after training. This was usually done by cutting the superior frontal to vertical lobe tract, but it is difficult in this way to isolate the whole vertical lobe without damaging the underlying centres. The vertical lobe was therefore removed from behind in some animals, although in all cases a small portion was left intact at the front end, avoiding the possibility of damaging other centres. The extent of lesion was examined after the experiment by serial sectioning. The procedures of operation and histological examination were as described by Boycott & Young (1955, 1956).

## MEMORIES PROMOTING ATTACKS ON CRABS

An octopus that has been freshly brought from the sea and placed in one of these tanks may or may not attack a crab or other figure shown a metre away, at the end distant from the home. A complicated set of factors is at work influencing the likelihood of attack; for example, disturbance during and after capture, hunger, and lack of familiarity with the tank. Animals were therefore kept for several days without the showing of any figures, fishes being given as food, in the home, six times a day.

After this period tests showed that attacks are not made equally readily by all octopuses or at all figures. For example, one octopus was given a series of tests with live crabs and various figures, shown in a random order, always with more than an hour between tests. Thus in one part of the series it was shown a black circle and waved its arms but did not leave the home; at the next trial a white horizontal rectangle, which it approached but did not attack. Then a white vertical rectangle, which was attacked, a black circle to which there was no approach at all, a white horizontal rectangle was approached, a white vertical rectangle this time elicited no approach but at the next trial a crab was shown and was attacked.

Altogether this octopus came out five times out of six (5/6) to attack crabs (which it was not allowed to catch and eat). It came out 3/6 times to attack a black rectangle (10 × 2 cm.) shown horizontally, which is a figure not unlike a large dark crab. Attacks were made 2/5 times on a white rectangle shown vertically, once each at a white and a black circle of 6 cm. diameter, but there was no attack at a black vertical rectangle or a white horizontal one. On the occasions when no attack was made within 30 sec. the octopus sometimes waved an arm at the figure from the home, or approached half way down the tank. Making a scale that awards 3 for an attack, 2 for an approach and 1 for waving the arms, the order of attractiveness of the figures appears as shown in Table 1.

It may be that other octopuses would show different orders of preference. An octopus that is being fed regularly in its home thus shows a tendency to put out the arms to attack moving objects appearing at a distance. This tendency is not very strong and is not the same for different objects, live crabs being attacked more often than the other figures tested.

If now the animal is rewarded as a result of attacks on any figure, the attacks at this figure will become more regular and the animal will come out much more quickly. This can be demonstrated by showing crabs and allowing the octopus to eat them (Fig. 1). The octopus in this experiment attacked and ate crabs on only four out of the first ten occasions when they were shown, but then on every occasion thereafter. Moreover, the times of the attack fell off in the following manner:

19, 6, 31, 15, 24, 17, 10, 7, 10, 5, 2, 3 sec.

During the latent period before the attack is completed the octopus may sit in the home showing signs of 'attention', or may move slowly down the tank towards the moving figure (Boycott & Young, 1950, 1955).

Table 1

| Figure | Attacks | Attacks + approaches, etc. |
|---|---|---|
| Crab | 4/5 | 14/15 |
| Black horizontal rectangle | 3/5 | 12/15 |
| White vertical rectangle | 2/5 | 8/15 |
| White circle | 1/5 | 8/15 |
| Black circle | 1/5 | 4/15 |
| White horizontal rectangle | 0/5 | 4/15 |
| Black vertical rectangle | 0/5 | 0/15 |

Although all octopuses probably attack and eat crabs in the sea, they have nevertheless to learn to attack them in the particular situation in the laboratory. They bring with them a system that makes attacks on crabs more probable than on other figures, but this only becomes 'strong' enough to produce regular and rapid attacks in the new situation when the attributes of that situation have also become associated with the crab as a food object. This is not merely a matter of 'becoming used to the tank'. Octopuses that have been trained to attack some other object at the end away from the home will still not regularly or rapidly attack a crab until they have been trained to do so (p. 719).

Conversely, when an octopus has become trained to attack crabs it will not necessarily attack all figures that are shown at the same place. Thus with the octopus of Fig. 1 a white circle of 6 cm. diameter was shown at irregular intervals as a test object (no reward or shock) during the period in which crabs were being given as food (first fifty trials). The circle was attacked three times out of the first five presentations and then only twice in the next ten, although throughout this period the octopus was regularly attacking crabs. The system is therefore such that a moving object not previously associated with food may be attacked, but the probability of attack is not high and it varies from animal to animal.

In the subsequent trials in Fig. 1 food was given when the octopus attacked the white circle (or after 15 sec. if it did not) and this object rapidly became a positive stimulus and was thereafter attacked regularly and with a short delay. Finally a second object, a circle of 2 cm. diameter, was introduced at alternate trials and shocks given when it was attacked. The attacks at this figure rapidly decreased in frequency; there was also at first a slight temporary lowering of the probability of attack on the larger circle, but then the discrimination was accurately performed.

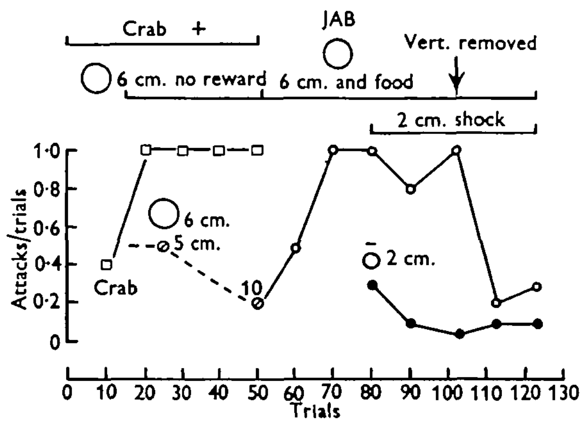


Fig. 1. For the first fifty trials the octopus was shown a crab and allowed to eat it if attacked. Beginning at the 15th trial a white 6 cm. circle was shown at irregular intervals and removed without reward if attacked. From the 50th trial onwards the crab trials were discontinued and the octopus was rewarded with fishes when it attacked the 6 cm. white circle. From the 80th trial a 2 cm. circle was introduced and shocks given if it was attacked. After the 100th trial the vertical lobe was completely removed, with some damage to the superior frontal lobe. Ordinates show the proportion of attacks in the previous ten trials, except that for the circle at the 25th trial the point represents five tests and at the 50th trial ten tests, spread irregularly over the previous period.

## ATTACKS ON A FIGURE WITH NEITHER REWARD NOR SHOCKS

In the experiments of Fig. 2 a black rectangle $10 \times 2$ cm. was shown six times a day and was withdrawn if attacks within 30 sec. were made, no reward or shock being given. The characteristic of the responses under these conditions is that they are irregular. The octopuses sometimes came out to attack, sometimes not, and the probability of attack fluctuated in a manner not easy to correlate with any other factor. Moreover, the attacks were slow. The animals were kept in as near as possible a constant state of hunger by feeding in the home with fishes six times a day. JDD attacked more often than JDA, but in both animals there were periods of several consecutive trials in which no attacks were made. Some memory reducing the probability of attack on a given set of attributes is thus set up by the mere absence of reward.

A convenient way of expressing the results given by an octopus over a period of trials is to divide the number of attacks by the total number of showings, giving an index of response estimated over the whole period. Since the value is not stable within the period, this index is not a probability in the strict sense. It provides an index of the behaviour that an octopus has shown under given circumstances.

After an initial period of learning the animal usually settles down to a steady performance, and an index calculated over this steady period would provide an estimate of the probable further behaviour of the animal. Nevertheless, the indices used have mostly been calculated over a fixed number of trials from the beginning of any given type of training. The index then gives an expression of the behaviour of the animal available for the making of comparisons with other animals (or the same animal under different conditions), provided that the number of trials con-

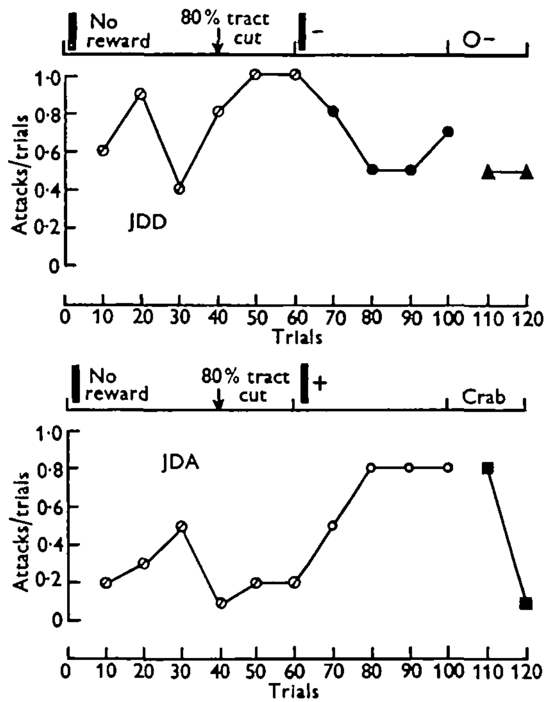


Fig. 2. During the first sixty trials a black verticle rectangle was shown and withdrawn without reward or shock if it was attacked. After the 40th trial 80% of the superior frontal to vertical tract was cut in both animals. In JDD after the 60th trial shocks were given if the black rectangle was attacked. After the 100th trial a white circle was shown and shocks given following attacks. In JDA after the 60th trial fish was given following attacks on the rectangle. After the 100th trial crabs were shown and shocks given if they were attacked.

sidered is the same. For octopus JDD this index was 0·78 and for JDA 0·28 for the parts of the experiments in which the black rectangle was shown and withdrawn without reward or shock.

After forty trials 80% of the superior frontal to vertical lobe tract was cut in these animals. The behaviour after operation was similar to that before, with a slightly greater tendency to attack, especially in octopus JDD. Every octopus has its own characteristic mannerisms and way of attacking in any given situation, for example JDA would move half way down the tank and wave its arms at the rectangle. This behaviour persisted after the operation.

It was then shown in octopus JDA that memories increasing the probability of attack can be set up after this injury to the vertical lobe. A fish was given when the rectangle was attacked (or after 15 sec. if it was not). The animal soon began to come out more regularly and quickly, but never on more than 8/10 trials, that is perhaps less regularly than in normal animals (Table 4, see p. 725). At the end of the experiment with JDA crabs were shown and the animal proved to come out readily to attack. It was not allowed to eat the crab but shocks were given following each attack. The attacks rapidly became less frequent, showing that a memory associating the crab with the shock can be built up even after removal of most of the vertical lobe. This result appears to contradict those found earlier (Boycott & Young, 1950, 1956), but the difference is that in the present experiment the octopus had never attacked and eaten crabs in the tanks. It is much more difficult to set up a memory preventing attacks if the crab has previously been made a positive figure (p. 724).

At the end of the experiment with octopus JDD shocks were given when the black rectangle was attacked and, as Fig. 2 shows, the attacks became less frequent, but still often occurred. With the vertical lobe damaged it is difficult to form a memory preventing attack on any figure. This was confirmed at the end of the experiment with octopus JDD by giving shocks when a white circle was attacked. Although this had never been a positive figure for this animal, attacks continued to be made on half the occasions. This shows clearly the value of the vertical lobe: in a normal animal a few shocks would be sufficient to prevent such attacks (p. 715).

The difference consistently shown throughout the experiments between JDA and JDD illustrates another characteristic feature. The probability of attack was always less in animal JDA than in JDD, either because of a hereditary difference or of a difference in the past experiences in the sea. Both animals were healthy throughout and readily ate the fishes given in their homes.

## EFFECT OF VARIOUS PERIODS OF LEARNING TO ATTACK ON SUBSEQUENT LEARNING NOT TO ATTACK

In order to test the effect of previous 'positive' training on the ease with which a memory not to attack a given set of attributes is set up, a series of octopuses was trained for varying periods to attack a black vertical rectangle 10 × 2 cm., by giving food when it was attacked, or after 15 sec. if no attack developed. After this 'positive' training the animals were given shocks when this figure was attacked, food being now provided in the form of fishes given in the home end of the tank.

### (i) *No previous positive training*

In octopus JEO, which serves as a base-line, there was no previous positive training (Table 2, and Fig. 3). The animal was isolated in the tank and fed from the beginning with fishes in its home. The black vertical rectangle was then presented at the opposite end of the tank and during the first ten trials three attacks were made and shocks received. Thereafter, during fifty further trials, spread over

8 days, there was only one further attack at this figure. Over the whole period the octopus only attacked four times, and we may therefore estimate its index of correct response as 56/60 = 0·93. It should be noted that this index is the reciprocal of that used on p. 712 to record the sequence of positive training. Tests with other figures then showed that this memory preventing attack was specific. A crab was attacked in 2/2 tests, a white 6 cm. circle in 3/3, and a black circle in 2/2. The only figure used that was not attacked was the 10 × 2 cm. black rectangle shown horizontally (0/2 tests).

Table 2. *Training not to attack a black vertical rectangle*

| Octopus | Previous positive trials | Correct responses | Index of correct response | Percentage vertical lobe removed or tract cut |
|---|---|---|---|---|
| | | A. Training before operation | | |
| JEO | 0 | 56/60 | 0·93 | — |
| JEP | 20 | 51/60 | 0·85 | — |
| JEG | 40 | 46/60 | 0·77 | — |
| | | B. Training after operation | | |
| JFI | 0 | 27/40 | 0·68 | 90 |
| JFA | 0 | 36/60 | 0·60 | 75 |
| JFC | 0 | 45/60 | 0·75 | 60 |
| | | C. Trained to attack before operation, not to attack after operation | | |
| JDQ | 20 | 39/60 | 0·65 | 50 |
| JDB | 40 | 46/60 | 0·77 | 40 |
| JDC | 80 | 35/60 | 0·58 | 75 |
| | | D. Trained to attack after operation, and then not to attack | | |
| JDT | 20 | 36/60 | 0·60 | 40 |
| JDR | 40 | 29/60 | 0·49 | 40 |
| JDS | 80 | 29/60 | 0·49 | 60 |

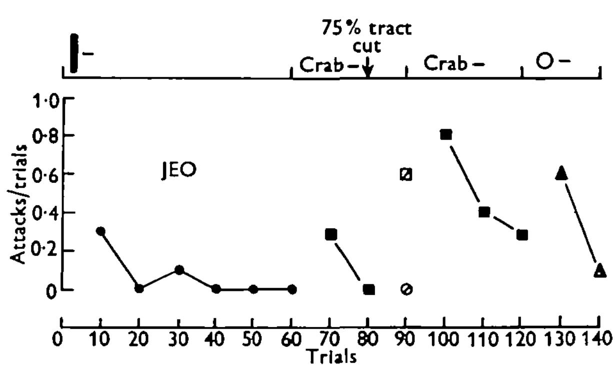


Fig. 3. Training not to attack a rectangle. For the first sixty trials a black vertical rectangle was shown and shocks were given if it was attacked. For the next twenty trials a crab was shown and shocks given following attacks. 75 % of the superior frontal to vertical lobe tract was then cut. Ten tests each were then given with the crab (▨) and black rectangle (⊘), no reward or shocks being given. From the 90th to the 120th trial crabs were shown and shocks given following attacks. From the 120th to 140th trial the white circle was shown, followed by shocks.

Over the next series of trials a crab was shown and shocks were given when it was attacked. After only three such shocks there were no further attacks in twenty trials. A memory preventing attacks on a crab is therefore readily set up if there has been no period of learning to attack crabs in this situation, and we may estimate the index of correct response as 17/20 = 0·85, though because of the difference in number of trials this index is not fully comparable with that for the black rectangle. Further tests showed the same conditions as before, circles being attacked, but neither the crab nor rectangle (crab 0/2, black vertical rectangle 0/2, black horizontal rectangle 0/2, white circle 2/2, black circle 2/2).

At this point 75 % of the superior frontal to vertical tract was severed. Tests showed that the memory preventing attacks on the crab had now been largely dissipated, but the tendency to attack persisted; attacks were made in 6/10 tests (without shocks). During the same period, however, the black vertical rectangle was never attacked. This shows at once the difference between the attributes of a crab and of other figures. Although crabs had never provided food in this situation they had presumably done so previously in the sea. A memory preventing attacks on them was readily set up while the vertical lobe was intact, but this was largely dissipated when the lobe was isolated. On the other hand, the memory preventing attacks at the black rectangle did not disappear after severance of the tract. This is a figure for which there was no previous memory and the representation of it in the optic lobes is held linked with the attributes of 'shock', even without the assistance of the vertical lobe. This experiment also shows that removal of the vertical lobe influence does not lead simply to a generalized tendency to attack all moving figures (see also Boycott & Young, 1956).

In the next series of trials with JEO shocks were again given when the crab was attacked. The attacks were much more persistent than before operation, the animal coming out 15/30 times, as compared with only 3/20. However, attacks became gradually less frequent, showing that a memory preventing attacks on crabs can be built up even after this injury to the vertical lobe, but that such a memory is much less rapidly established than in the normal animal and tends to dissipate, leaving an irregular performance. The index of correct response has fallen from 0·85 before operation to 0·50 afterwards.

The white circle, however, was still attacked (Fig. 3), showing that the memory partially preventing attacks on crabs was specific. Shocks given with the white circle then led to a decrease in attacks on it, the rate of learning being greater than when training not to attack crabs, but slower than the original learning by the intact animal not to attack the black rectangle. The vertical lobe therefore also plays some part in learning not to attack figures not previously associated with food.

At the end of this long series of trials associated with shocks the octopus rarely came out to attack any figure, but did not otherwise appear inhibited or withdrawn, often putting out an arm when the figure first appeared.

The above conclusions find confirmation in further experiments. Thus in another octopus (JDP) shocks were given from the beginning when a black vertical rectangle was attacked and this figure rapidly became negative, there being in all six attacks in forty trials, four of them in the first ten. Tests then showed that crabs and white circles were still attacked, but not a black horizontal rectangle.

### (ii) *Reversal after positive training*

In two normal octopuses, before giving shocks, short periods of training to attack the black rectangle were given, the animals being rewarded with fishes. Fig. 4 and Table 1 show that in octopus JEP, in which there were twenty initial

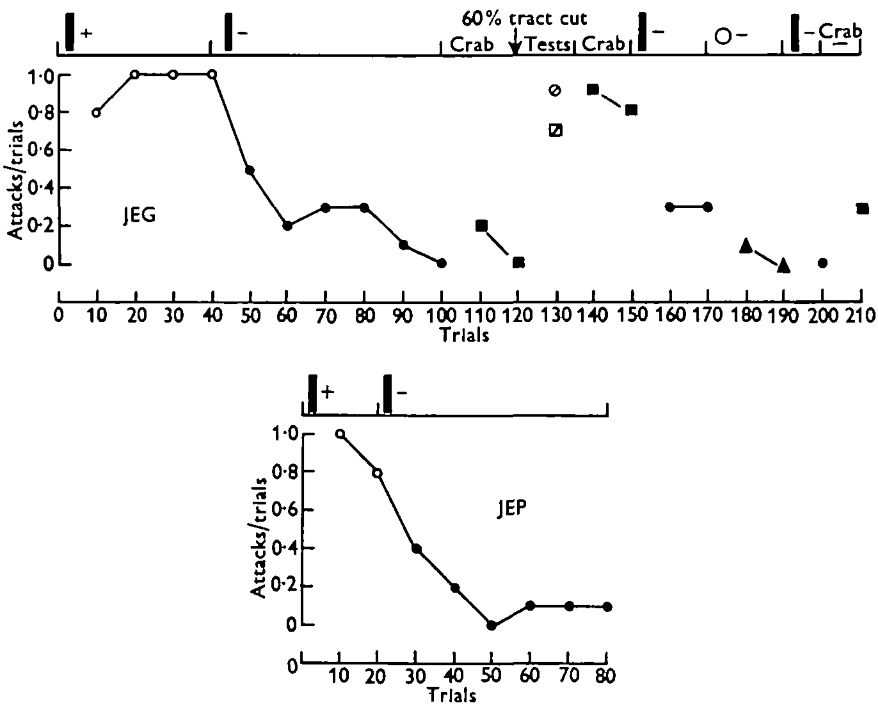


Fig. 4. Training first to attack and then not to attack a rectangle. In JEP there were twenty and in JEG forty initial trials in which fish was given when the rectangle was attacked. For the next sixty trials in both animals shocks were given after the rectangle was attacked. In JEG there were then twenty trials in which a crab was shown and shocks given if it was attacked. 60 % of the superior frontal to vertical lobe tract was then cut. After ten tests each with the crab (⧄) and rectangle (⊘) without reward or shock there were then twenty trials with the crab followed by shock and then twenty with the rectangle and shock. From the 170th to the 190th trial a white circle was shown and shocks given. For the next ten trials the rectangle was shown but never attacked. Finally, in the last ten trials crabs were shown and shocks given.

training trials, the black rectangle was attacked nine times in spite of shocks, in the subsequent sixty trials ($I = 0{\cdot}85$). In octopus JEG, with forty initial trials, there were fourteen such attacks ($I = 0{\cdot}77$). The animal JEO, with no initial 'positive' training (p. 714), only attacked four times in sixty 'negative' trials ($I = 0{\cdot}93$). It is thus clearly shown that it is more difficult to set up a memory preventing attack on a figure that has been previously associated with food (see Table 2). Both JEP and

JEG, when they had learned not to attack the vertical rectangle, readily attacked crabs. Evidently the crab, although it had never provided food in this situation and had not been seen at all for 10 days, provided a strong positive stimulus.

Octopus JEG continued to attack other figures when it had finally learned not to attack the black vertical rectangle. It even attacked the same rectangle shown horizontally. The memory preventing attack can therefore be highly specific for one set of attributes.

At this stage (trial 100, Fig. 4) shocks were given when JEG attacked crabs, and a memory preventing attack was set up so rapidly that only two attacks were made in twenty trials ($I = 0{\cdot}90$). Now 60 % of the vertical lobe tract was cut. Tests without reward or shock immediately thereafter showed numerous attacks on both the crab and the black vertical rectangle. In octopus JEO (Fig. 1), where the rectangle had never been a positive figure, elimination of the vertical lobe did *not* lead to attack on the rectangle. The contrast with JEG is striking and suggests that the vertical lobe plays an especially important part in maintaining memories that prevent attacks in situations that have been previously associated with food.

The setting up of a memory preventing attacks on crabs now proved nearly impossible in octopus JEG, there being attacks on 17/20 occasions ($I = 0{\cdot}15$). The black rectangle was, however, easily again made negative (6/20 attacks, $I = 0{\cdot}70$), and finally the white circle, which had never been a positive figure, was attacked and shocked only once in twenty trials. The ease with which memories preventing attack are set up by animals with reduced vertical lobe tissue thus depends upon the extent to which the figure concerned already constituted a positive stimulus. The series is uncontrolled, however, in the sense that shocks were given first with the crabs and last with the white circle. However, further tests (trials 190–210) then showed that the result was not due simply to this sequence of presentation. Crabs still proved able to elicit more attacks than any other figure.

(iii) *Setting up of memories preventing attack after operation on the vertical lobe*

(*a*) *No positive training*

In the next series the animals were operated at the beginning of the experiment, after a period of 2 days in the tank during which they were fed with fishes in the home. During this time tests were made with various figures, the animal being neither rewarded nor shocked if it attacked them (see p. 710). After operation, when the black vertical rectangle was presented, it was attacked and shocks given, the experiment being continued as usual for sixty trials. Fig. 5 and Table 2 B show that attacks were much more numerous than in intact animals. JFA made 24/60 attacks and JFI 13/40 ($I = 0{\cdot}60$ and $0{\cdot}68$). In JFA there was no improvement during the course of the experiment, attacks were made about four times in each ten trials, sometimes at several consecutive trials, with periods of no attacks sometimes as long as nine trials. At the end of the series of trials with JFA further tests showed that the octopus would usually come out to attack a crab, but would only put out an arm or approach towards other figures. Finally shocks were given when the octopus came out to attack crabs. The animal slowly learned not to attack (see p. 724). In a third octopus, JFC (Fig. 5 and Table 2), crabs were shown immediately after operation and shocks given if they were attacked. The animal continued for sixty trials to attack on about 4/10 occasions (p. 724). In the next sixty trials the black vertical rectangle was shown and shocks given. Attacks were rather less frequent than on the crab, but still occurred on many occasions ($I = 0{\cdot}75$). Memories preventing such attacks are much less reliable after these lesions than in a normal animal (Table 2).

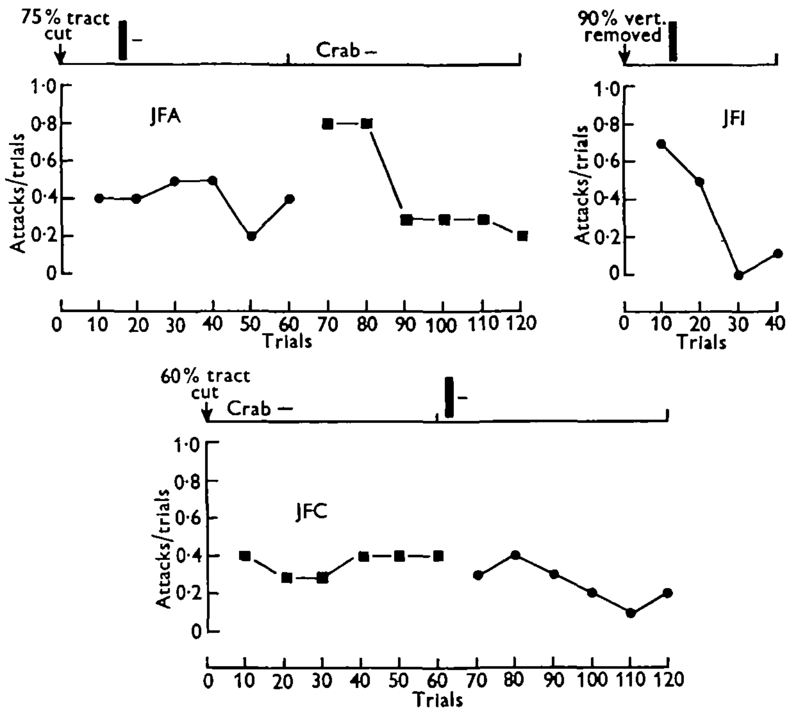


Fig. 5. Learning not to attack after vertical lobe lesions. Lesions were made at the beginning of each experiment. In JFA and JFI a black vertical rectangle was shown in the subsequent trials, shocks being given if it was attacked. JFC was trained not to attack crabs in the first sixty trials after operation. Subsequently it was trained not to attack the rectangle.

### (*b*) *After positive training before operation*

Three octopuses were trained for twenty, forty and eighty trials, to attack the black vertical rectangle before operation. When this positive response had been established tests were made with crabs and other figures and these were usually attacked, but always after much longer delay than when the rectangle was shown. For example, octopus JDB, after forty trials with the black vertical rectangle, rewarded by fishes, came out regularly within 3 sec. to attack that figure. When a crab was shown the octopus remained for 10 sec. moving its head up and down in the home, then put out an arm and moved on to the top of the bricks. Waving the arms towards the crab it moved slowly half-way down the tank and finally dashed at the crab 27 sec. after it had appeared. This is clearly a positive reaction, but not a strong one such as is given to the black vertical rectangle. The memory producing attacks at the latter was quite specific and the same rectangle, when shown horizontally, was not attacked (three trials). This demonstrates very clearly that a specific memory ensuring attack on the rectangle had been established, making it a more 'attractive' figure in this situation even than crabs, which had presumably provided food in the sea.

The vertical lobe tract was then partly cut and after this operation the octopuses continued to emerge to attack the black vertical rectangle more readily than crabs or other figures. Memories ensuring attack thus survive this operation and correct performance of attacks does not involve the integrity of the vertical lobe. Shortly after operation shocks were given when the rectangle was attacked, food being provided by giving fishes at the home end of the tank. Fig. 6 and Table 2 C shows that far more attacks were made than by the intact animals of Table 2 A. These animals in Table 2 C tended to show more attacks in the early period and there was a gradual improvement, but the total number of attacks in sixty trials is similar to that shown by JFA and the other animals in Table 1 B. Unfortunately the differences in the extent of interference with the vertical lobe system make exact comparisons difficult and do not allow us to say exactly how the amount of preoperative positive training influences the ease with which memories preventing attack on a given figure are set up without the vertical lobes.

JDQ, the animal with the least amount of positive training in this set, rapidly stopped attacking when shocks were given, but then began again for a period. Only half of the vertical lobe tract had been cut and at the end of the sixty negative trials this animal attacked the black vertical rectangle only rarely. Tests then showed regular attacks on crabs and a white 6 cm. circle, but not on a rectangle shown horizontally.

The animal was next shown to be readily made negative to both the white circle and to the crab, one shock sufficing in each case to prevent attacks for the subsequent nine trials. Even an animal without a complete vertical lobe can thus quickly form memories preventing attack on figures that are not already strongly positive. During the next twenty trials the octopus was allowed to eat crabs when it attacked them. After this period of positive training a negative memory preventing attacks on crabs was then set up only with much greater difficulty. The animal attacked seven times in the first ten trials in spite of the shocks received. After thirty trials attacks on the crab fell almost to zero, but for the whole thirty trials the index of correct response was only 0·63. Over the first ten trials it was 0·30 as against 0·90 before the positive training with the crab. Tests with the white circle and black rectangle showed attacks on nearly all occasions. The memories attached to these figures had faded and they were not involved in the specific memory preventing attacks on crabs.

Octopus JDB, with forty positive trials before operation, shows essentially the same sequence, but became 'negative' rather more easily than JDQ in spite of the greater amount of positive training; fourteen attacks were made in sixty trials ($I = 0.77$), only 40 % of the tract had been severed. As before it was then found that slow attacks were made upon crabs or a white circle, but these were very rapidly inhibited by shocks. The white circle was then made into a positive figure by rewarding with fishes when it was attacked (or presenting them with the figure if no

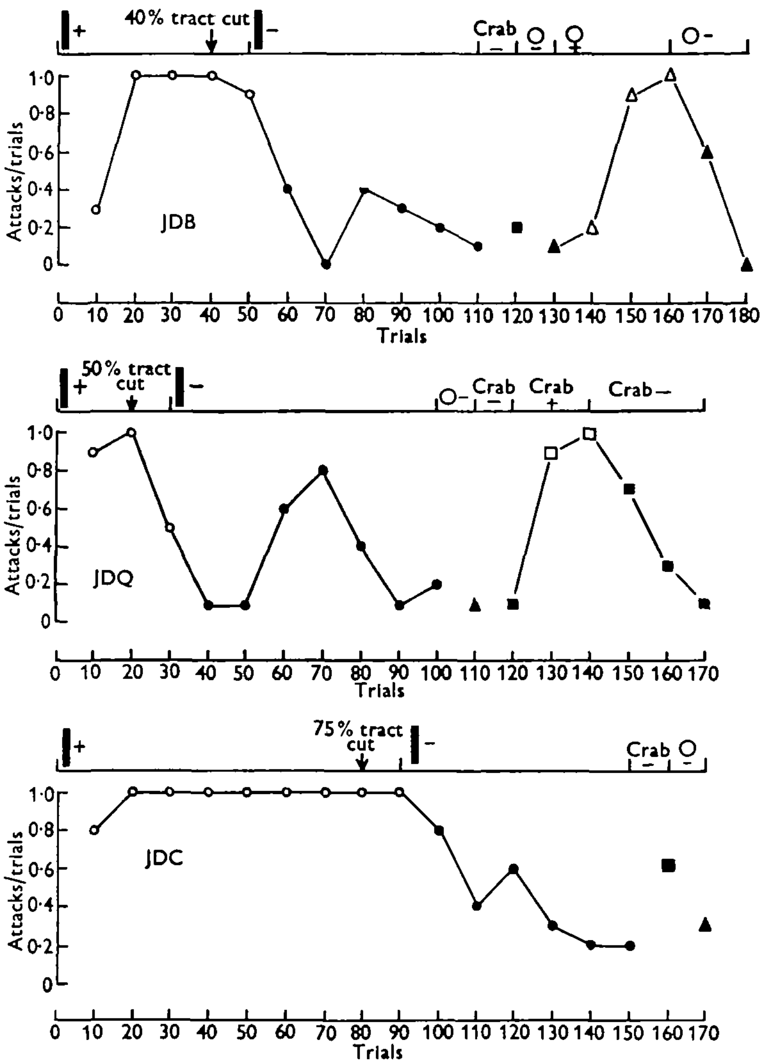


Fig. 6. Learning to attack before a lesion, and then not to attack after. The animals were given first respectively forty, sixty and eighty positive trials with reward. They were then operated and given sixty negative trials, with shocks if they attacked. JDQ was then given ten negative trials, each with a white circle and a crab. From the 120th to 140th trials it was then allowed to eat the crabs, but from here onwards shocks were again given if a crab was attacked. JDB, after the sixty negative trials with the rectangle, was given ten negative trials each with crabs and a white circle, and then from trials 130 to 160 the white circle was made positive by rewards. Finally shocks were again given for attacks on the circle. In JDC the experiment was ended by ten negative trials, each with crabs and the circle.

attack developed in 15 sec.). After thirty trials a positive response was well established (showing that the complete vertical lobe is not necessary for this). Crabs shown at this time were not attacked; the negativity attached to their attributes had persisted for 8 days, the positive factor becoming attached only to the white circle. Shocks were then given when the white circle was attacked, which occurred six times in the first ten trials, a marked contrast to the one attack in ten before positive training. However, after these six shocks the white circle was not further attacked; a memory preventing attack on it had been developed in spite of the injury to the vertical lobe. Finally tests showed that the black rectangle was now no longer a negative figure. It had not been shown for 9 days and the original positive effect attached to it had returned. Moreover, there was evidence that the specific memory of the set of attributes 'black vertical rectangle' had survived, for a rectangle shown in the horizontal position was also not attacked.

JDC was the member of this set with the greatest amount of positive training before operation (eighty trials). The memory ensuring attack survived interruption of 75% of the tract and was reversed only very slowly by shocks. There were twenty-five attacks in sixty trials, mostly in the early stages ($I = 0{\cdot}58$). There was definite improvement in performance, but mistakes were made even at the end. After this time there were attacks on crabs or a white circle; the negativity partially attached to the rectangle was specific.

### (c) *Training to attack after section of the superior frontal to vertical tract*

In a further three animals the operation was performed as soon as they had become accustomed to the tanks and the positive training was then given (Fig. 7 and Table 4). The learning to attack was in each case rather slow, the total number of attacks in the first twenty trials for these three animals taken together being 42/60 as against 50/60 for the animals in the last section, which were trained before operation. This suggests a possible effect of the vertical lobe on the setting up of positive memories (see p. 727), but further experiments are needed. There were some signs that in the early stages of positive training the memory that ensures attack lasted only for a short time. These attacks were made more regularly at tests given an hour after previous tests than at the first trial of the day. Such 'short memories' are a conspicuous feature of learning not to attack in animals with no vertical lobes (Boycott & Young, 1955).

Tests at the end of the period of positive training showed that the octopus would come out to attack crabs or other figures, but less regularly and more slowly than to attack the rectangle. Thus in JDS the order of 'positive' effect was black vertical rectangle > crab = white circle > black horizontal rectangle.

The training not to attack then followed the same course as in the animals made positive before operation (Table 2 D). In all three octopuses it was difficult to reverse the positive tendency, even though it had been set up after operation. Indeed the number of attacks was greater in this series than in the previous one, although the lesions were smaller. Signs of the effect of the amount of positive training appeared in the fact that the animal with only twenty positive trials attacked twenty-four times in the subsequent sixty trials ($I=0{\cdot}60$) as against thirty-one times ($I=0{\cdot}49$) for each of the animals with forty and eighty positive

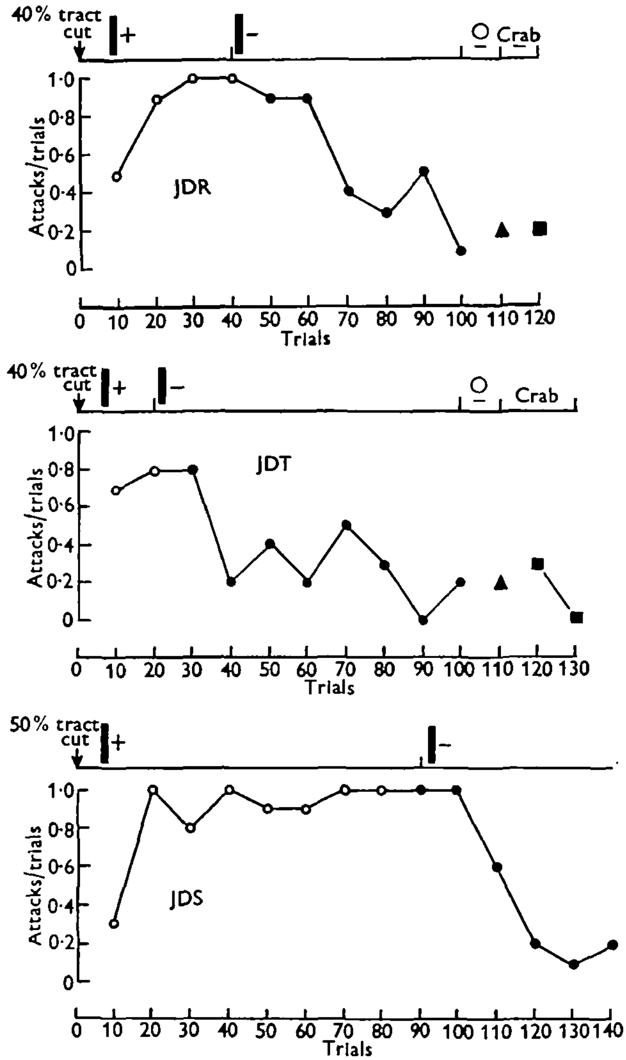


Fig. 7. Training after lesions, first to attack and then not to attack. All the animals were operated at the beginning of the experiment. They were then given twenty, forty or eighty positive trials with the rectangle followed by reward. Each was then given sixty trials in which attacks were followed by a shock. The experiments were ended by negative trials with a white circle and with crabs.

trials. The proportion of attacks given by these animals trained positively after operation was similar to that in the previous series trained before operation (Table 2 C, D). Differences in the extent of lesion make close comparison difficult, but there is a suggestion that the memories set up *after* operation are more difficult to reverse. Thus JDS attacked at every one of the first twenty negative trials in spite of the shocks received. However, by the end of sixty trials attacks had become rare ($I = 0{\cdot}49$ for the whole period).

The outstanding feature that emerges from the four series in Table 2 is that animals with impaired vertical lobe function learn only slowly not to attack a previously positive figure, and that their performance is erratic.

At the end of sixty trials the black vertical rectangle was attacked only seldom by the animals of series 2 D, but attacks were still readily made on a white circle or on crabs. By means of shocks this positivity was then readily reversed, as in the previous series.

## EFFECT OF PREVIOUS TRAINING ON SETTING UP OF MEMORIES PREVENTING ATTACKS ON CRABS

It has already been shown that a normal octopus can readily be trained *not* to attack crabs (Boycott & Young, 1955). There has been no systematic investigation of the effect of the amount of previous *positive* training on the later learning not to attack. Octopus JFG (Fig. 8) shows that with no previous positive training the memory preventing attack is quickly set up in a normal animal—there were only three

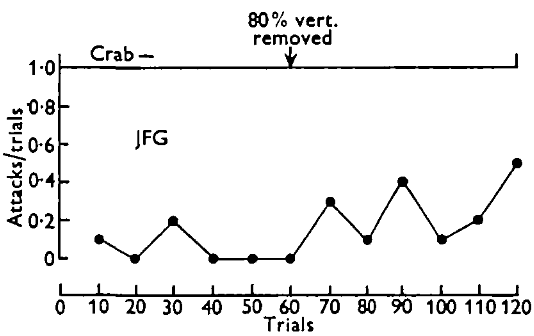


Fig. 8

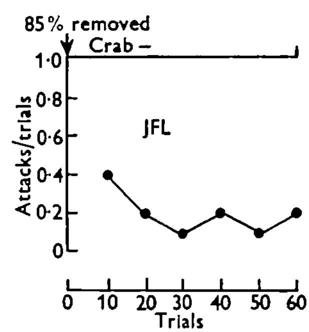


Fig. 9

Fig. 8. Octopus trained not to attack crabs for sixty trials and then 80% of vertical lobe removed. The attacks became more frequent.

Fig. 9. 85% of vertical lobe removed immediately the animal arrived in the laboratory and the octopus then trained not to attack crabs for sixty trials.

attacks in sixty trials ($I = 0{\cdot}97$). The vertical lobe was then removed (80%) and the animal attacked more often, but still only 16/60 times ($I = 0{\cdot}73$). Such memories can therefore be maintained without the intact vertical lobe.

In three octopuses the vertical lobe tract was partly cut, or the lobe removed, immediately after the animal arrived in the laboratory and shocks were then given when crabs were attacked (Figs. 5, 9). Over the next sixty trials in JFC (60% cut), there were twenty-two attacks, either three or four in each ten trials, without any systematic improvement ($I = 0{\cdot}63$). Similarly, in JFA (75% cut) there were 27/60 attacks at the crab ($I = 0{\cdot}55$). In JFL (85% removed) there were only 12/60 attacks ($I = 0{\cdot}80$, Fig. 9), which is still, however, more than would be made by a normal animal (Table 3).

Table 3. *Responses of octopus when shocks are given when crabs are attacked*

| Octopus | No. of positive trials | Correct responses | Index of correct response | Percentage vertical lobe removed or tract cut |
|---|---|---|---|---|
| A. No previous training to attack crabs | | | | |
| JEO | — | 17/20 | 0·85 | 0 |
| JEG | — | 18/20 | 0·90 | 0 |
| JFG | — | 57/60 | 0·97 | 0 |
| JFA | — | 48/60 | 0·80 | 85 |
| JFG | — | 44/60 | 0·73 | 80 |
| JFA | — | 33/60 | 0·55 | 75 |
| JEO | — | 15/30 | 0·50 | 75 |
| JDC | — | 4/10 | 0·40 | 75 |
| JFC | — | 38/60 | 0·63 | 60 |
| JEG | — | 3/20 | 0·15 | 60 |
| JDQ | — | 9/10 | 0·90 | 50 |
| JDB | — | 8/10 | 0·80 | 40 |
| JDT | — | 7/10 | 0·70 | 40 |
| JDR | — | 8/10 | 0·80 | 40 |
| B. With previous training to attack crabs | | | | |
| JFB | 40 | 33/60 | 0·55 | 70 |
| JDQ | 20 | 3/10 | 0·30 | 50 |
| JDE | 100 | 13/40 | 0·32 | 35 |
| JED | 100 | 35/60 | 0·58 | 20 |

Table 4. *Responses to positive training with black vertical rectangle*

| Octopus | Attacks | Index of response | Percentage tract cut |
|---|---|---|---|
| A. No training | | | |
| JDD | 27/40 | 0·68 | — |
| JDA | 11/40 | 0·28 | — |
| B. With positive training | | | |
| JEP | 18/20 | 0·90 | — |
| JEG | 38/40 | 0·95 | — |
| JDQ | 19/20 | 0·95 | — |
| JDB | 33/40 | 0·82 | — |
| JDC | 78/80 | 0·98 | — |
| C. With positive training after cutting tract | | | |
| JDA | 31/50 | 0·62 | 80 |
| JDR | 34/40 | 0·85 | 40 |
| JDT | 15/20 | 0·75 | 40 |
| JDS | 69/80 | 0·86 | 60 |

In a number of other operated animals the effect of giving shocks when crabs were attacked was tested, without previous positive training. The results are summarized in Table 3, arranged in order of completeness of removal of the vertical lobe. All the animals learned more slowly than the three normal octopuses shown at the top of the table. However, there is considerable variability among the operated group. Some of those with the larger lesions gave a fairly accurate performance and vice versa. Octopus JEG, for example, with 40 % of the vertical lobe intact, attacked on nearly all occasions, giving an index of correct response of only 0·15, whereas JFL with only 15 % intact gave 0·80. The explanation of these differences may lie in the history of the animals before coming to the laboratory, some having been more particularly crab-eaters than others. Evidently the vertical lobe is involved in setting up memories that prevent attacks on crabs, but it is not essential that the lobe be intact if the crab has not been learned as a positive figure in this situation.

In animals that had learned to attack crabs in the tanks it was in general more difficult to set up memories preventing attack on crabs after vertical lobe injury. Thus JFB, with 70 % of the tract cut (Fig. 10), was given forty trials in which it was

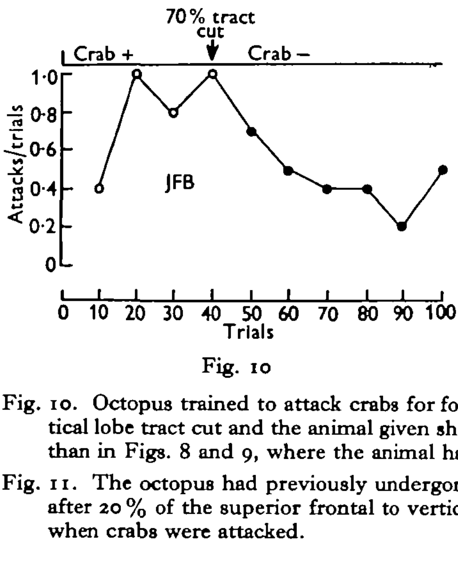


Fig. 10

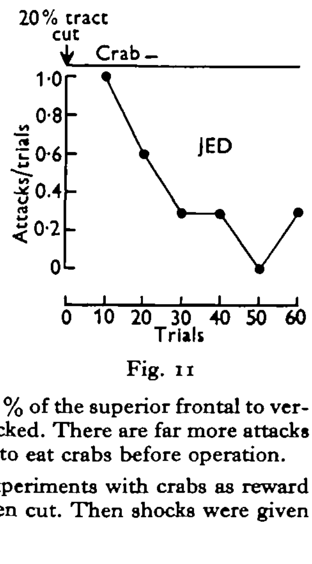


Fig. 11

Fig. 10. Octopus trained to attack crabs for forty trials and then 70 % of the superior frontal to vertical lobe tract cut and the animal given shocks if crabs are attacked. There are far more attacks than in Figs. 8 and 9, where the animal had not been allowed to eat crabs before operation.

Fig. 11. The octopus had previously undergone a long series of experiments with crabs as reward after 20 % of the superior frontal to vertical lobe tract had been cut. Then shocks were given when crabs were attacked.

allowed to eat the crabs and the vertical lobe was then removed. Shocks were then given whenever crabs were attacked and there were found to be 27/60 attacks ($I=0·55$). Other animals confirmed this finding: JDQ (p. 720) gave $I=0·30$ after twenty positive trials with crabs. Octopus JDE had been used in a long series of experiments in which crabs had been given as reward. Although only 35 % of the vertical lobe tract had been cut the animal attacked on 27/40 occasions on which it was shown crabs and shocked if they were attacked ($I=0·32$). Similarly, in octopus JED, after a long series of experiments with crabs as reward, subsequent to 20 % section of the vertical lobe tract, the animal was trained not to attack crabs. It showed gradual improvement, but attacked on 25/60 occasions, $I=0·58$ (Fig. 11). These experiments do not show precisely the effect of various amounts of positive training on the setting up of memories preventing attacks on crabs. They show that even with vertical lobes nearly intact such memories are formed only with difficulty and are liable to break down, the positive response tending to reappear. Memories having some effect in preventing attacks on crabs can be set up after removal of most of the vertical lobe using intervals of about 2 hr. between trials. However, the operated animals behave much less 'correctly' than normal ones in this situation, and it is especially difficult to prevent attacks on crabs if the octopus has been allowed to eat these while in the tank.

## DISCUSSION

Feeding an octopus in its home for some days and then testing its response to figures shown at the other end of the tank provides a useful technique for revealing the capacities that the animals bring with them from the sea. The result may be expressed by saying that they tend to attack any small figure moving in the visual field, but the probability of attack within a given time is less than one, and varies from octopus to octopus. Although there has been no very thorough investigation, the evidence is that not all figures are equally likely to be attacked; crabs and horizontal rectangles are attacked more often than other figures (p. 710), the horizontal rectangles perhaps because they resemble crabs. An octopus therefore brings from the sea a store of information associating certain visual attributes with food. The effect of this memory in ensuring attack is not very strong, but after crabs have been attacked and eaten in the tank the probability of attacks on them greatly increases. Similarly, other figures, which are at first only sometimes attacked, will be attacked regularly after they have been associated with food. Conversely, if a crab or other figure has never been associated with food in the tank, then if shocks are given when it is attacked a memory preventing attack upon it is readily set up, but this is much more difficult if the figure has become associated with food.

There is some evidence that the memory associating a given set of attributes with food resides in the optic lobes. After considerable amounts of the vertical lobes have been removed an octopus comes out to attack crabs more readily than other figures (p. 716). The neuronal system that had been previously set up representing the association of the attributes of a crab with food was not disturbed by the operation—presumably because it resides in the optic lobes. However, animals with vertical lobe functioning impaired learn the positive association between a given figure and food rather more slowly than normal (Table 4). The vertical lobe is therefore involved in the process of setting up 'positive' memories in the optic lobe, by which the attributes of a situation are associated with food. It would be interesting to repeat this experiment with removal of larger amounts of the vertical lobes.

The present series provides clear evidence that the vertical lobe plays a part in setting up memories that associate a set of attributes with a shock. This effect is seen even if the figure had never previously been associated with food. Thus the operated animals of series B in Table 2 learned not to attack a black rectangle more slowly than did JEO of series A. If a figure has been previously associated with food, then it is more difficult for an operated animal to store the information that associates it with a shock. The animals in series C and D of Table 2 learned less well than those in series B, though the difference is complicated by the variation in the amount of tissue remaining. The vertical lobe may thus be especially involved in the setting up of memories that prevent attack on previously positive figures. The fact that after vertical lobe removal the animals tend to make mistakes in the direction of attacking in spite of shock has previously led to the suspicion that these lobes are especially involved in the storage of associations with shock (Boycott & Young, 1956). However, in many of the experiments reported in earlier papers the situations studied all included crabs, which the octopus were allowed to eat and which were therefore 'positive' figures.

The present series contains decisive evidence that removal of the vertical lobe does not lead simply to indiscriminate attacks on all figures, but only on those that had previously been 'positive'. Thus octopus JEO (Fig. 3) after operation came out to attack crabs, but not to attack a black vertical rectangle. Conversely, JEG (Fig. 4), in which the rectangle had been made first positive and then negative, came out to attack both crabs and the rectangle after operation.

The vertical lobes are thus involved in the setting up and maintaining of visual and tactile associations (Wells & Wells, in preparation). They are not, however, essential for either setting up or maintenance of the memories. In the present series JFL, JDA, JFO and JFA, with less than a quarter of the lobe remaining, all showed some capacity to store information preventing attack on crabs. Performance was, however, very much less accurate than in normal animals. If animals with no vertical lobe remaining may yet store 'negative' memories for short periods this strongly suggests that the appropriate neural configurations can be set up in the optic lobes alone and that the vertical lobes tend to reinforce and maintain them.

## SUMMARY

1. Octopuses were fed for some days with fishes in their homes at one end of the tank, and the effect of figures shown at the opposite end was tested.

2. Any small moving object may then be attacked, but the probability of attack is low and the delay long.

3. Crabs and a black horizontal rectangle were attacked more often than other figures. If a figure is withdrawn on the occasions when it is attacked, then the probability of attacks remains low and may slowly decrease.

4. If the octopus is allowed to eat crabs the probability of attacks on them quickly rises towards unity. If food is given when some other figure (say a black vertical rectangle) is attacked, then this figure will later be attacked. An octopus makes attacks more regularly on a figure that has recently been associated with food than on any other figure.

5. This learning to attack a given figure can take place after removal of most of the vertical lobe, but the learning is slower and responses less accurate than in the normal animal.

6. Octopuses from which the vertical lobe has been removed attack crabs more readily than other figures. The system that ensures attack therefore resides elsewhere, probably in the optic lobes.

7. If shocks are given when a previously neutral figure is attacked, then the probability of further attacks on this figure rapidly approaches zero. Attacks on other figures or crabs remain frequent. If the vertical lobe is then removed, no attacks are made on such an originally neutral figure.

8. If a figure that has been associated with food is then rewarded with shocks, the probability of attack falls more slowly than if the figure had been neutral. If the vertical lobe is now removed, the frequency of attacks rises. The memory preventing attack is therefore partly resident in the vertical lobe.

9. The greater the amount of previous training to attack, the more slowly does the animal learn not to attack. This applies also if the training to attack is given after vertical lobe removal.

10. After vertical lobe removal, shocks given when crabs are attacked rapidly reduce the probability of attack if the octopus had not previously eaten crabs while in the laboratory. If such feeding had taken place, the probability of attack falls only slowly without the vertical lobes.

11. The experiments show that information stores associating a given figure with either food or shock can be set up after removal of the vertical lobes but tend to dissipate more rapidly than in a normal octopus.

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