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SHORT AND LONG MEMORIES IN *OCTOPUS* AND THE INFLUENCE OF THE VERTICAL LOBE SYSTEM

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INTRODUCTION

It is clear that the paired centres of the vertical lobe system are an important part of the memory system of an octopus, but it remains uncertain how they operate (Young, 1965). There is some evidence that the effects of removal of the median superior frontal and vertical lobe are different (Young, 1964; Nixon & Young, 1966). In the present work this difference has been further investigated, using the method of following the rise and decay in tendency to attack after showing a figure and rewarding with food or shock. By studying the results of single learning occasions in this way it is possible to analyse the unit processes that are involved (Young, 1960). It will be shown that the median superior frontal and vertical lobes have somewhat different effects both on the increase in attacks at a figure produced by food and the decrease produced by shocks.

METHODS

Octopuses were obtained and kept individually in plastic tanks, by the methods described elsewhere (Wells & Young, 1968). After some days in the laboratory they were operated upon under urethane anaesthesia. The operations, distributed roughly randomly among the animals, were:

(*a*) controls, in which the cranium was opened and the jelly around the brain removed;

(*b*) removal of the median superior frontal lobe;

(*c*) removal of the vertical lobe.

The animals were of 200–400 g., and of both sexes.

Studies of learning to attack were made by showing a grey horizontal rectangle 10 cm. × 2 cm., moved vertically on a transparent plastic rod at the end of the tank distant from the 'home' of the animal.

An attack was recorded only if the animal touched the rectangle, and the time from presentation was taken with a stopwatch. When required, a piece of fish was given on the end of a metal rod. The trial was ended if there had been no attack within 20 sec. In some trials in order to increase the tendency to attack all the animals were fed, those that had not attacked being given food after the 20 sec. The rectangle was moved down the tank and the fish was shown near to it and close to the octopus in its home. The animal could then be lured out and made to follow the rectangle and the piece of fish down to the far end of the tank, where it was allowed to seize the fish.

The animals with various operations were mixed in the row of tanks so that the experimenter did not know which operations had been performed, though this became evident later from the numerous attacks made by some of those without vertical lobes.

The effect of shock was studied by showing a crab on the end of a thread and giving a shock if it was attacked (8 V. a.c.).

All the experiments consisted in showing either the rectangle or the crab associated on one or more occasions with food or shock and then later testing whether the animals attacked them, but without giving further food or shock. At these test trials the rectangle was pulled away as it was touched, and the crab just before it was seized. What is studied therefore can be considered as the process of building up of a tendency to attack the rectangle and the subsequent decay of this tendency by the lapse of time, perhaps assisted by extinction.

Altogether fifteen animals without vertical lobes, twelve without median superior frontal lobes and twelve controls completed the trials. These were not of course all done at the same time, but divided between three batches within a few weeks of each other so that any variations in conditions were randomized. The temperature was 23–25° C.

The extent of the lesions was checked by serial sectioning at the end of the experiments. The amount of vertical lobe removed was 80–95% with the exception of one animal with 60% removed. There was some damage to the top of the anterior subvertical lobe in two animals and the posterior subvertical lobe in five others. There was no clear correlation of differences in behaviour with these differences in lesions so they are not reported in detail.

The amount of median superior frontal lobe removed varied from 60 to 100%, without appreciable damage to other tissues. Again there was no obvious correlation of behaviour with amount removed. The greater part of the superior frontal to vertical tract had been severed even when some of the median superior frontal lobe was intact.

RESULTS

1. *Learning to attack a rectangle*

On the day after operation all the animals were first tested with the rectangle, shown twice at 5-min. intervals. After the second showing all were fed a piece of fish near to the rectangle as explained on p. 385. Of the normal animals and those without vertical lobes 40–50% came out at the initial trials, whereas none of those without median superior frontal lobes attacked. Then, at intervals after the feeding, tests with the rectangle alone were given. In Fig. 1 the attacks at 5 min. and 10 min. are shown together as a single point, as are those at 25–40 min. A further point shows the responses at times up to 2 hr. after the feeding. Many animals in the normal group and in the group without superior frontal lobes attacked more often after feeding than before, but the animals without vertical lobes did not show this response. The effect declined steeply.

Eight hours later on the same day the animals were tested again. Initially attacks by the normals and those without median superior frontal lobes had fallen to a very low level, those without vertical lobes remained as before. Food was given, followed by tests, showing markedly increased responses after feeding, as at the morning session.

A similar sequence was followed on the second day, except that in the evening two feedings were given, and so also on the third day. On the fourth day there were four feedings. In this way the changes in behaviour after feeding with the rectangle were followed. On every occasion the control animals responded with a large increase in number of attacks, until eventually all were attacking on some occasions. At first the level of attack then declined markedly during the subsequent hours from its peak. Later it became more stable until most of the control animals attacked regularly from the first trials of each session onwards.

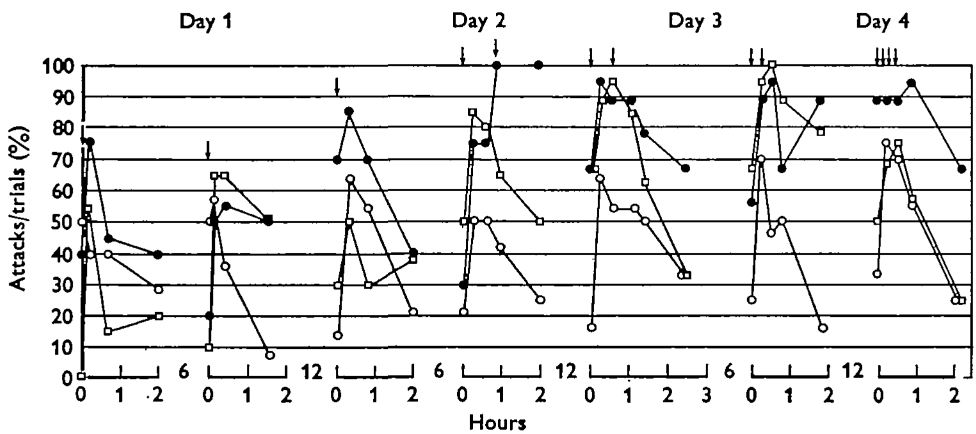

Fig. 1. Learning to attack a horizontal rectangle. At each of the points shown with an arrow all the animals were given food with the shape. At all the other trials there was no reward for attacks. Each point represents the proportion of attacks made by the animals at two trials. Closed circles, 12 control animals; open circles, 15 without vertical lobes; squares 12 without median superior frontal lobes ●, Normal; ○, no vertical; □, no median superior frontal lobes.

The animals without median superior frontal lobes mostly increased their attacks to about the same level as the controls. The fall at subsequent trials was, however, markedly quicker. In those without vertical lobes the rise in attacks after feeding was usually less than in either of the other groups and the fall was even faster than in those without superior frontal lobes. It is clear that interruption of the vertical lobe circuit lowers the effect of food in establishing a tendency to attack an unfamiliar figure. This is confirmed by a further series with the rectangle at the end of the experiment (p. 391). Part at least of the reason for this failure is the curtailed duration of the short memory ensuring attack after feeding.

2. *Learning not to attack crabs*

On the fifth day of the experiment all the animals were shown a crab attached to a thread, and given a shock if they attacked it. This test was repeated twelve times at exactly 5-min. intervals. The eleven remaining control animals (one had escaped) all came out at the first two trials but attacks then fell off sharply, so that at the eighth trial there was only one attack (Fig. 2 and 3). One of the animals continued to attack for all twelve tests. Only three others attacked at more than half the tests, the quickest learners being those with only four attacks. The mean was 6·6 attacks.

The animals without median superior frontal lobes all attacked at the first three tests (Fig. 3), and thereafter attacks decreased much as in the control animals (Fig. 2). The tendency to attack was, however, distinctly stronger than in the latter. Two out of eight aminals attacked every time, three more at more than half the tests. The mean was 7·9.

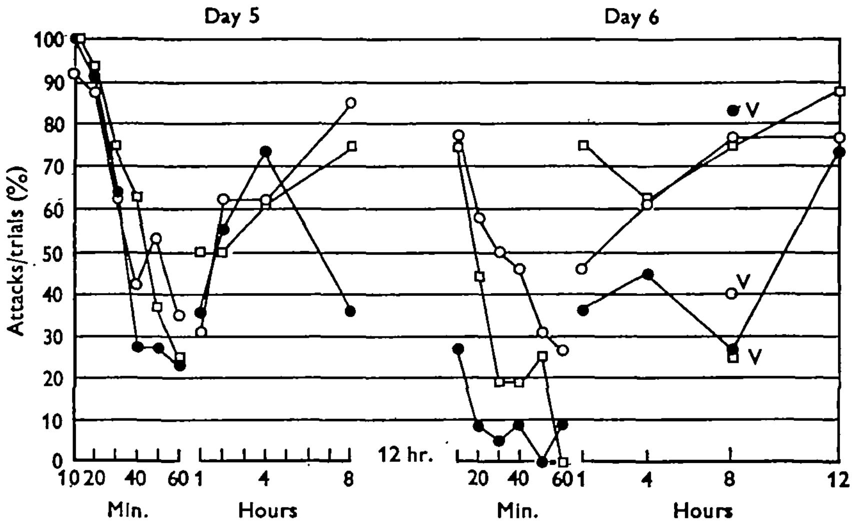

Fig. 2. Effect of shocks on attacks at crabs. On each day the animals were shocked for attacks during the initial period, marked in minutes. Tests were given every 5 min. and each point shows the results for two consecutive tests. The later tests, during the periods marked in hours, were given without shock, the crab being simply withdrawn before it could be seized. Symbols as for Fig. 1. At the points marked V a vertical rectangle was shown.

The thirteen animals without vertical lobes all attacked at the first test. Thereafter some were irregular, though the general tendency to attack was high. None attacked every time, but all except three at more than half the tests. The mean was 7·4 attacks. The individuals tended to stop attacking for one or two trials and then to attack again (Fig. 3). The mean performance of the group was irregular and they persisted more than the other groups in attacks at the end of the session (Figs. 2 and 3).

3. *Return of tendency to attack crabs*

The persistence of the inhibition on attacks was tested by showing crabs to the animals 1 hr., 2 hr., 4 hr. and 8 hr. after the sessions with shocks. The crab was pulled away before the octopus seized it, but no further shocks were given. Recovery of attacks followed approximately the same course in all three groups during the first 4 hr., but after 8 hr. whereas the two groups with removals attacked at 80% of the tests, the controls had returned almost to the minimum level. The significance of the large number of attacks by the control group after 4 hr. is not clear. Certainly the effect of the shocks lasts longer in these animals. This appeared most markedly when trials were continued on the following day, the animals being shown crabs on a series of twelve further trials with shocks if they attacked. Only four of the control animals

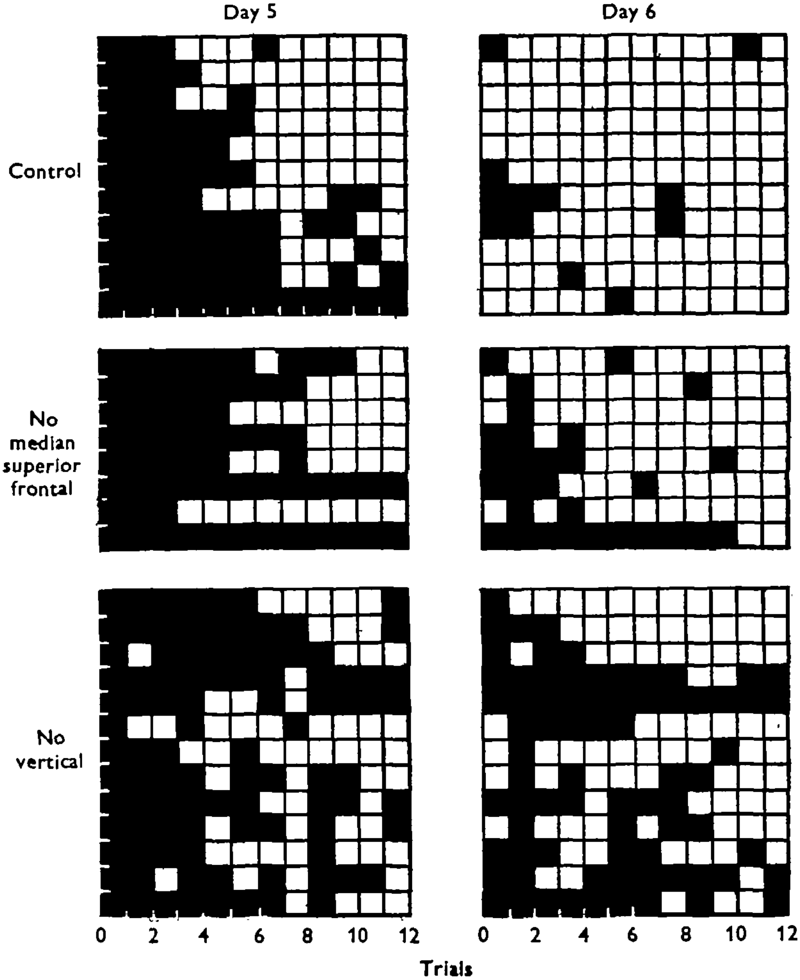

Fig. 3. The records for the individual animals during the twelve trials on days 5 and 6 when they were shocked for attacks at crabs. Each filled square represents an attack. On day 6 five of the control animals made no attacks at all.

came out, even at the first trial and very few further attacks were made (Figs. 2 and 3) The mean number of attacks was 1·2, the maximum being four and five animals not attacking at all.

The animals without median superior frontal lobes began by attacking at about 75% of the first two trials. The attacks then fell off rapidly and reached zero for the last two trials. The maximum was ten attacks, by one animal, but no others attacked at more than half the tests. The least was one attack. The mean was 3·6. Clearly these animals had retained some inhibition from the previous day, but much less than the control animals ($P = < 0{\cdot}01$, Wilcoxon's non-parametric).

Those without vertical lobes showed even less retention. They began by 77% of attacks for the first two trials. The level then fell much more slowly than when only the median superior frontal lobe was removed, and never reached zero for the group. One animal attacked at every trial, six out of thirteen attacked at more than half the trials. One attacked once only (it had attacked seven times on the previous day). The mean of attacks was 5·8. These animals, too, therefore showed some signs of retention but much less than the controls. Comparison with those without median superior frontal lobes is difficult because of the large spread in number of attacks in both groups. The distribution of the attacks is more different than the total number (Fig. 3). Those of the animals without vertical lobes continued to the end of the series, whereas the animals without superior frontal lobes attacked much at first but stopped completely before the end of the series. This is the pattern that would be expected if the presence of the vertical lobe is necessary to allow effective inhibition of attack.

After the series of twelve trials with shocks the animals were tested with crabs at intervals of 1, 4 and 8 hr. and again the following morning. Both the operated groups showed more rapid recovery of attacks than the controls (Fig. 2). The latter had, however, returned to a high level of attacks at crabs by the morning of the seventh day, by which time of course the majority of them had received no shocks for 2 days. The inhibition of attack was specifically to crabs and did not prevent attacks at a vertical rectangle by over 80% of the control animals (Fig. 2). Conversely this figure was attacked very little by either of the operated groups, which had failed previously to learn to attack rectangles.

4. *Intensive training to attack*

The sequence was ended by a series of four sessions on days 7 to 9 at which the animals were again shown the horizontal rectangle and given food with it whether or not they had made an attack. At the first session there were six trials, later eight. The control animals initially attacked at 60% of trials, increasing later to around 80% (Fig. 4). They began the next session at 70% and went to 90% and in the third reached 95%. At the fourth they were a little lower, perhaps from overfeeding.

The animals without median superior frontal lobes throughout attacked rather less than the controls. Their attacks generally increased during the session but reached levels rather lower than the controls.

The group without vertical lobes began by making much fewer attacks than either of the other groups. Throughout they attacked consistently less than those without superior frontal lobes. Their attacks increased during the sessions but dropped markedly between, so that they began the last session with only 30% of attacks. Clearly learning to attack is as severely impaired by this lesion as learning not to attack.

DISCUSSION

These results provide further insight into the function of the vertical lobe circuit as a whole and especially of the vertical lobe itself. Removals can never be very informative about the median superior frontal lobe alone, because all its output is through the vertical lobe (Young, 1970).

The process of learning to attack an unfamiliar figure involves a short-lasting increase in tendency to attack, some residue of which remains as long-term learning (Young, 1964). The increase occurs in animals with the vertical lobe circuit interrupted but declines more rapidly than in controls. This rapid decline was somewhat more marked in those without vertical lobes than in those without median superior frontal lobes, but it is doubtful if the difference is significant. In the last of the tests in Fig. 1 the two groups are precisely parallel. In the final experiment shown in Fig. 4 those without median superior frontal lobes seemed to have learned more than those without vertical lobes, but the difference is not great. It remains uncertain therefore whether the presence of the vertical lobe alone is able to help in promoting learning to attack. Further experiments with removal of both lobes are planned to investigate this.

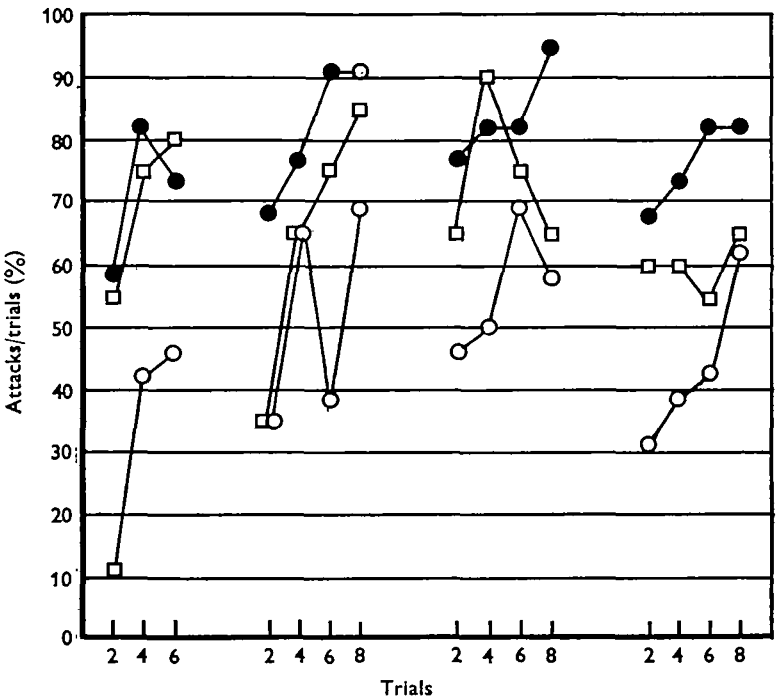

Fig. 4. Intensive training to attack a horizontal rectangle on days 7–9. At every trial the animals were given food with the rectangle, even if they had not attacked it. Each point shows the results of two consecutive trials. ●, Normal; ○, no vertical lobes; □, no median superior frontal lobes.

Although neither group of operated animals had learned well to attack rectangles they both very readily attacked crabs, and continued longer than controls to do so when shocked. Moreover, when tested later the animals with the vertical lobe circuit interrupted showed much less retention of the inhibition to attack. Those without vertical lobes were much more seriously affected than those without median superior frontal lobes (Fig. 3). This is very valuable evidence that the vertical lobe can exert an inhibitory effect even in the absence of its median superior frontal lobe input. After the operation it still retains an input from below, presumed to be of pain fibres. When suitably activated (by shocks) this remaining system is still able to produce some degree of inhibition of the tendency to attack and to allow some record of this to be 'printed', presumably in the optic lobe. A greater reduction of effect of shocks after removal of vertical than of median superior frontal lobes has already been suspected (Young, 1964; Nixon & Young, 1966).

The inhibitory effect elicited after removal of the median superior frontal lobe cannot be pre-synaptic, since the fibres of the superior frontal to vertical tract have gone. This of course does not show that pre-synaptic inhibition does not occur, but it must mean that in addition there are ways in which the cells of the vertical lobe can be activated to have an inhibitory influence elsewhere in the system.

In the absence of the vertical lobe the effect of shocks in restraining attacks at crabs is short-lived. It is significant that half of these animals were still attacking intermittently at the end of the series of twelve trials with shocks (Fig. 3). Nevertheless, some longer-lasting effect was still apparent, even the next day.

This process of learning not to attack a familiar food object is a useful experimental device, but it is in some ways an 'unnatural' situation. The tendency to attack crabs is not permanently lost, at least with the number of shocks here applied. Yet while it lasts the inhibition is apparently specific to the crab configuration. The control animals readily attacked a rectangle at a time when they would not attack crabs (Fig. 3). The effect of the vertical lobe system in this situation is not simply to produce a general depression of the tendency to attack. There must be specific inhibition of the previously established system that promotes attack at the crab configuration. It is difficult to see how this can be explained by a model such as the mnemon, especially since the inhibition is reversible.

The present experiments show very clearly that in the absence of the vertical lobe the duration of the effects both of food and of shock are curtailed. This agrees with the view that this system operates by increasing the tendency to attack and for food to accentuate this tendency *unless* some signals of trauma intervene. The fact that the lobes are arranged to form a circuit with the optic lobes suggests that the prolongation of effects they produce may be due to reverberating cycles. The internal feed-back through to the lateral superior frontal lobes would have the same effect. The physiology of these circuital systems remains to be investigated. Like the circuits of the vertebrate limbic system their functions are related both to positive and negative rewards and to the changes that take place in learning.

SUMMARY

1. Octopuses from which either the median superior frontal or the vertical lobes have been removed show reduced capacity to learn to attack an unfamiliar figure.

2. The duration of the increased tendency to attack after feeding is reduced by both operations. This suggests that the failure to learn is due to interruption of a self-re-exciting circuit.

3. Although these operated animals would not attack rectangles they continued to attack crabs for much longer than controls, in spite of shocks. They also retained signs of this inhibition less well.

4. When the median superior frontal lobe alone had been removed the remaining vertical lobe was able to exercise considerable restraint by virtue of its input from below.

5. This shows that the effect of this lobe in preventing attack at a particular figure cannot be wholly due to pre-synaptic inhibition, since the effect can appear when the relevant pre-synaptic fibres are absent. The 'pain' fibres are therefore able to activate

the vertical lobe to produce inhibition of the system that produces attack at a particular shape.

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