LEARNING AND OTHER FUNCTIONS OF THE HIGHER NERVOUS CENTRES OF *SEPIA*[1]

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INTRODUCTION

SURPRISINGLY little is known about the function of the higher nervous centres of invertebrates. Although much has been discovered about the capacity for learning and other more complex modes of behaviour especially among insects, yet there has been little attempt to reveal the activities within the central nervous system by which such reactions are mediated. This is especially regrettable because of the possibility offered by these centres of discovering something of the changes which occur during the process of learning, which in spite of so much study in vertebrates still remains almost wholly obscure (see Lashley, 1937). Yet in this subject, where great difficulties arise from the special and complex arrangements of the vertebrate nervous system, there is some expectation that comparative studies will yield fruitful results.

The central nervous system of the Cephalopods is especially well suited for such work. The supra-oesophageal centres are large, and there is reason to believe that the behaviour is complex and likely to include interesting types of learning. Moreover the animals lend themselves well to experiment, and the parts of the central nervous system are easily accessible for the purpose of operation.

Divisions of central nervous system

The main divisions of the central nervous system of the Dibranchiate Cephalopods are the paired optic lobes, and the supra- and sub-oesophageal ganglia (Fig. 1). However, each of these major regions is subdivided internally into lobes, which are the true structural and functional units. Some, though not all, of these lobes have been previously described and named (see especially Dietl, 1878: Thore, 1939); but details of their internal structure and fibre connections remain obscure, as does the part which each plays in the behaviour of the animal. For present purposes we may recognize centres of four types, as follows.

Lower motor lobes. The sub-oesophageal ganglia consist mainly of large neurons whose axons run, either directly, or after one further synapse, to

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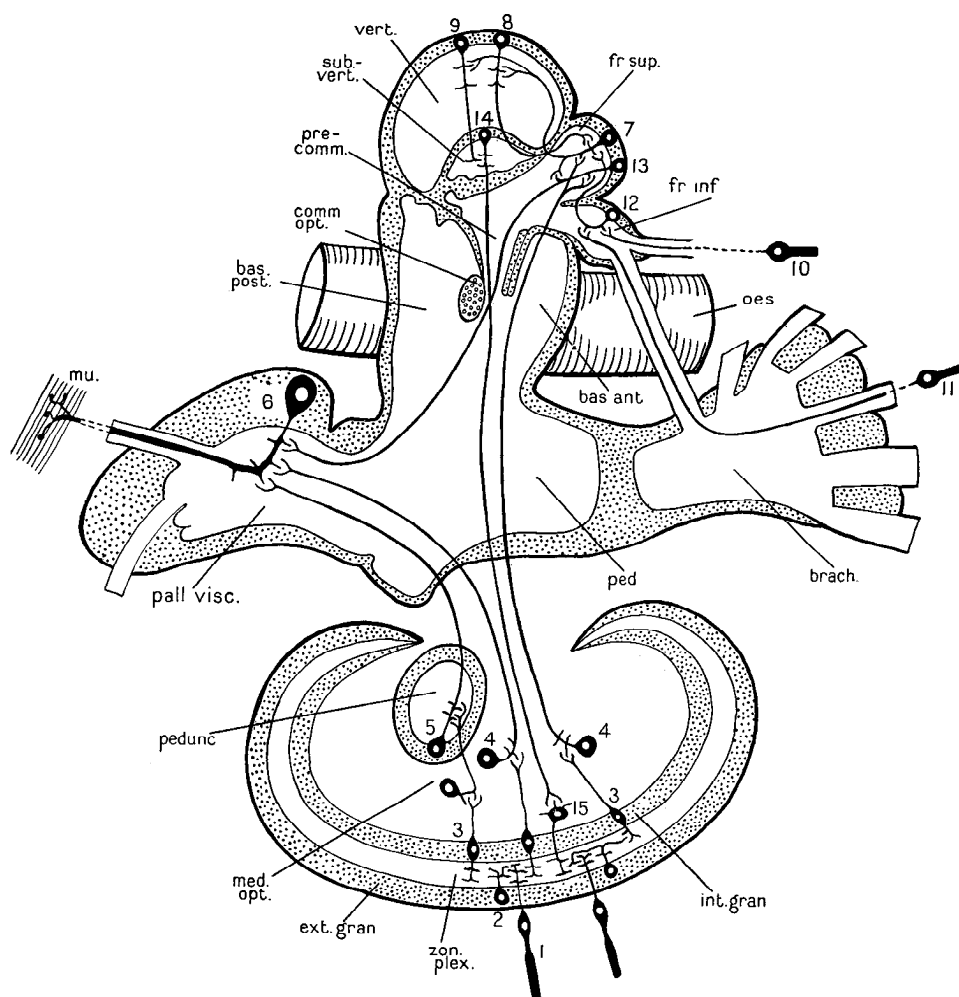[3] Fellow of Magdalen College, Oxford.

FIG. 1. Diagram to show some of the connections of the verticalis complex of *Sepia*, and its reciprocal relations with the optic lobes. The main outlines drawn from a single sagittal section, but the optic lobes much schematised.*

1, retinal cells; 2, external amacrines; 3, bipolar cells; 4, efferent cells of optic lobe; 5, cell of l. pedunculi; 6, final motoneuron; 7, cell of tractus frontalis superior-verticalis; 8, cell of tractus verticalis-frontalis superior; 9, cell of tractus verticalis-subverticalis; 10, visceral afferent; 11, tactile or chemoreceptory cell of arm; 12, cell of l. frontalis inferior; 13, cell of tractus frontalis superior-precommissuralis; 14, cell of tractus subverticalis-opticus; 15, centrifugal giant cell of internal granular layer.

(*Legend continued on next page*)

* The diagram is based mainly on the work of Cajal (1917) for the optic lobe and original data for the rest. The arrangement is certainly close to that shown but there is still some uncertainty about the following points: a) the exact form of the bipolar neurons 3; b) the connections of the efferent tracts of the lobus pedunculi 5; c) the relations of the sensory tracts 10 and 11 with the neurons 12, and of 7 with 13; d) the connections of the efferent tracts of the lobus frontalis superior 13.

muscles or other effectors (Fig. 1). Thus the arms and tentacles are controlled from the brachial and pedal ganglia, the funnel and eye-muscles from the pedal ganglia, and the mantle, fins and some of the viscera from the pallio-visceral ganglion. Electrical stimulation of these centres produces movements of the part innervated, and the movements are local, not synergic. In addition to the large motor neurons, these regions also contain smaller ones whose processes do not extend beyond the lobe itself. Sensory fibres from the skin also end at this level, and the centres are certainly able to act reflexly. After removal of one of these lower motor centres the part innervated is completely and permanently deprived of motor innervation.

The motor neurons of such regions may thus be considered comparable to the ventral horn and other parts of the somatic motor column of a vertebrate, and the lower motor centre as a whole, receiving afferent fibres and containing 'association' and motor neurons, is functionally not unlike the spinal cord.

Higher motor lobes. The more ventral part of the supra-oesophageal ganglia consists of lobes containing neurons of intermediate size, whose axons run to the lower motor centres. In this category are the lobus basalis anterior and posterior (Fig. 1 and 2), a hitherto unrecognised lobe the basalis lateralis, and the lobus pedunculi (= "ganglio del pedúnculo óptico" of Cajal, 1917), situated on the optic tract. All of these regions receive many fibres from the optic lobes and they may be considered as higher motor centres. Electrical stimulation of any of them causes movements of large groups of muscles, and after their unilateral removal circling and other forced movements of the animal take place, often in the form of continuous activity, as if their absence had freed the lower centres from an inhibition (Young, unpublished).

The influence of these lobes may therefore be compared in a general way with that of the regions of the mammalian brain which affect the 'tone' of

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(Continued from preceding page)

bas. ant.; lobus basalis anterior.
bas. post.; lobus basalis posterior.
brach.; ganglion brachiale.
comm. opt.; optic commissure.
ext. gran.; external granular layer of retina profunda.
fr. inf.; lobus frontalis inferior.
fr. sup.; lobus frontalis superior.
int. gran.; internal granular layer of retina profunda.
med. opt.; medulla of optic lobe.
mu.; muscle.
oes.; oesophagus.
pall.-visc.; palliovisceral ganglion.
ped.; pedal ganglion.
pedunc.; lobus pedunculi.
precomm.; lobus precommissuralis.
subvert.; lobus subverticalis.
vert.; lobus verticalis.
zon. plex.; zona plexiformis of retina profunda.

lower centres, for instance the red nucleus and other parts of the extrapyramidal motor system.

Primary sensory centres. These include the regions directly connected with the main afferent systems, and serving to elaborate the patterns of impulses sent from the periphery. The optic lobes, and especially their outer portions, the 'deep retina' (Fig. 1), are the most conspicuous formations to be placed in this section, but there are also olfactory lobes on the optic stalk (Young unpublished), and perhaps other regions which could be considered of the same nature. This type of centre is not always clearly marked off from
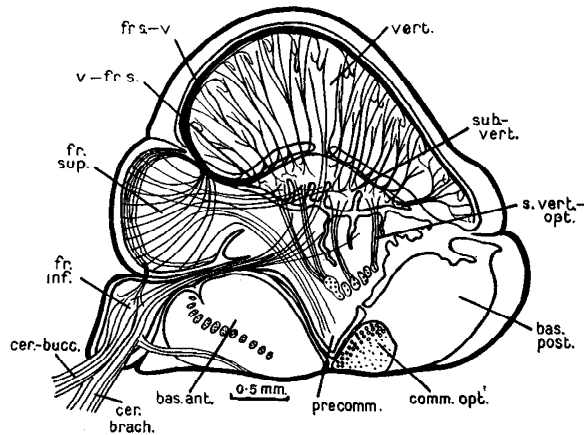

Fɪɢ. 2. Semi-diagrammatic view of median sagittal section of supra-oesophageal ganglia of *Sepia*. Outlines drawn from a single section, details schematic.
    cer-brach.; cerebro-brachial connective.
    cer-bucc.; cerebro-buccal connective.
    fr. s.-v.; tractus frontalis superior-verticalis.
    s. vert.-opt.; tractus subverticalis-opticus.
    v.-fr. s.; tractus verticalis-frontalis superior.
    Other lettering as in Fig. 1.

the previous one. The function of such a centre is to allow interaction between the impulses coming from the various parts of the receptor with which it is connected, so that reaction to shape or other qualities of stimulation may take place (see Young, 1938). Faradic stimulation of the centre of the optic lobe of *Sepia*, from which the processes of large cells pass to both supra- and sub-oesophageal regions (Fig. 1), produces definite movements, such as a general darkening or movements of the mantle or fins. But faradisation of the outer portion of the lobe usually produces no movements, presumably because so crude an agent as this stimulation is unable to simulate that patterned mode of activity by which this region normally controls the lower neurons.

Correlation centres. The highest centres, occupying the top of the supra-oesophageal ganglia, consist of very small cells, and are not directly connected with any single receptor or with the lower motor centres. These are the lobes with which the present work is mainly concerned, namely those

called by Dietl (1878) lobus frontalis superior and lobus verticalis, and the region below the latter which will here be called lobus subverticalis (see Fig. 2). These three are intimately connected, and may be collectively called the *verticalis complex*.

It was shown by Bert (1867) and von Uexkull (1895) that these regions are 'silent' areas, whose electrical stimulation produces no motor response. This has been confirmed in *Sepia* during the present work. Faradic stimulation of the lobus verticalis or frontalis superior with a monopolar electrode and a strength of shock considerably greater than that which produces responses from the lower centres produces no visible movements or changes of colour. The results of such experiments must however be accepted with some reserve, since it is possible that the brief shocks produced by an inductorium are unsuitable for stimulating such small fibres.

Study of the connections of the verticalis complex of ganglia throws further light on their function as 'higher centres' since it shows:—(i) that they provide opportunity for the interaction of impulses from various receptor fields; (ii) that they have no direct connections with lower motor centres; (iii) that there are elaborate reciprocal connections between and within the lobes such as would allow of the presence of self-re-exciting chains of activity (see Young, 1938).

Connections of lobus frontalis superior. The mechansim for the interaction of sensory impulses of various types is well seen in lobus frontalis superior (Fig. 1 and 2). This is approximately of kidney shape, as seen in sagittal section, having a thick layer of cells over its anterior surface. The axons of these cells run across the neuropil which occupies the centre of the lobe, and here they are crossed by layers of fibres from sensory sources, producing a characteristic criss-cross appearance. The tracts entering the lobe come from at least four sources, namely:—(i) optic lobes; (ii) skin of arms and tentacles; (iii) receptors around the mouth and perhaps from the gut, by way of buccal ganglia, *(iv) lobus verticalis (see below). The discharge of the fibres issuing* from lobus frontalis superior is presumably controlled by the combined action of these various sets of fibres, though the exact manner of the interaction, and the significance of the positions of the various layers, remain very interesting subjects for future investigation.

The fibres emerging from the 'hilus' at the hind end of lobus frontalis superior divide into three bundles passing to (i) lobus verticalis; (ii) lobus subverticalis; (iii) higher motor centres at the base of the supra-oesophageal ganglia by way of an undescribed region to be called lobus precommisuralis (Fig. 2).

Connections of lobus verticalis. The opportunities for the formation of self-re-exciting chains of activity are well illustrated by the connections of lobus verticalis (Fig. 1 and 2). This has a thin outer layer and a very large central mass of neuropil. The axons of the cells of the outer layer run downwards across the neuropil, giving off numerous axonic collaterals, and then collect into bundles which pass through into lobus subverticalis and either

end there or turn forwards to form the tract running to lobus frontalis superior which has already been mentioned. The main bundle of fibres entering lobus verticalis is that which arises in lobus frontalis superior. The two lobes can thus certainly influence one another reciprocally, and it is not unlikely that they can do so continuously, setting up a self-re-exciting system. The exact courses of tractus frontalis superior-verticalis and tractus verticalis-frontalis superior which complete the chains are shown in Fig. 3.

The existence of this type of circular connection was the starting point of the experiments to be described below, since it was suggested (Young, 1938) that possibly the cycle of activity is set up when impulses from various afferent sources interact, and that the maintenance of such cycles constitutes the
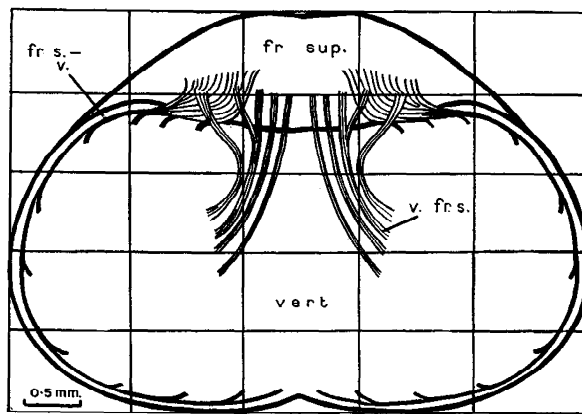

Fig. 3. Horizontal view of l. frontalis superior and l. verticalis of *Sepia*, showing the tracts connecting them with each other. For explanation of the co-ordinates see p. 503. Lettering as in Fig. 1 and 2.

basis of learning. It is not necessary here to recapitulate the details of the scheme originally proposed, but it may be noted that in addition to the cycle between lobus frontalis superior and lobus verticalis, the anatomical arrangements allow for a second and larger one, enclosing the first. For fibres from the lobus subverticalis run to the optic lobes, from which, as already explained, a large bundle passes to lobus frontalis superior. The activities of the verticalis complex can thus influence the discharges of those neurons of the optic lobes which run to the suboesophageal centres either direct or via lobus pedunculi.

The existence of these reciprocal connections must be of fundamental importance in the working of the centres, but it must not be forgotten that in the masses of neuropil lie many cells whose axons do not extend beyond the limits of the lobe in which they arise. The activities of such complex centres can hardly be wholly described in such simple terms as those employed above, which interpret all nervous function in terms of propagated nerve impulses. Yet perhaps no fundamental modification of the scheme pro-

posed would be necessary should we come to understand that masses of nervous tissue such as the neuropil of these lobes function by giving local rather than propagated responses when impulses are fired into them, such local responses serving to change the thresholds of the efferent fibres which issue from the mass.

Our purpose in the present work has been to make a first exploration of the functioning of these regions by the crude methods of stimulation and extirpation. In particular we have attempted to discover what effect on the behaviour, and especially on the powers of learning, is produced by the removal of lobus verticalis, or such part of it as would prevent its reciprocal excitation with lobus frontalis superior and stop the self-re-exciting chains described above.

The results so far obtained do not allow of a complete answer to the questions, but they show clearly that some at least of the more complex capacities of *Sepia* (such as that of following its prey out of the field of view) depend on the integrity of these highest supra-oesophageal centres.

Previous work on behaviour and learning in Cephalopods

In addition to the elaborate organisation of the central nervous system, the Cephalopods possess highly developed sensory and motor systems, and it is generally agreed that they show a complex or 'higher' pattern of behaviour. Unfortunately there has been very little attempt to justify this estimate by detailed observation or classification of the acts of which the animals are capable.

The 'higher' qualities of behaviour may be said to include:—(i) wide sensory and motor capacities, that is to say the ability to respond to varied aspects of the surrounding situation and to make this response in varied ways; (ii) the power to pursue an objective by indirect means, for instance to take a devious route in order to obtain food, or otherwise to show 'intelligence' in the solution of problems; (iii) the possession of conspicuous capacity for learning, *i.e.*, allowing the functional state of the nervous system to change so that present response is modified by past experience.

The wide sensory and motor powers of the Cephalopods are well known and need no further comment. It is with the second and third of the above types of capacity that we are here concerned. There are very few reliable data about the ability of the Cephalopods to obtain their ends by indirect means. Pieron (1909) claimed that Octopods are able to uncork a bottle in order to obtain crabs seen through its glass wall, and similar statements are frequently made in semi-scientific literature. Unfortunately in no one case has sufficient detail or documentation been given to show whether the interpretations applied are correct. The observations detailed below show that *Sepia* is certainly able to follow a prawn which has moved out of its visual field, a by no means simple type of behaviour.

The data about the learning powers of these animals are slightly more satisfactory. Mikhailoff (1920) and Kühn (1930) have shown in Octopods

that formation of simple conditioned reflexes is possible, touch being the unconditioned stimulus used for conditioning coloured lights to produce chromatophore changes or flight reactions. Kühn was able to show that discrimination depending upon both wavelength and intensity is possible. Von Uexkull (1891) claimed that Octopods which have once attempted to eat crabs covered by Sea Anemones not only never do so again but actually refuse all further food. However, this remarkable conditioning is denied by Polimanti (1911).

The capacity to discriminate between visual shapes is highly developed, the eyes being well suited to the purpose (Alexandrowicz, 1927; Heidermanns, 1928). Tinbergen (1939) has recently shown, by studying the responses of *Sepia* to models of the opposite sex, that colour pattern as well as type of movement determines sexual recognition. It is highly probable, though no experiments have been made on the subject, that the prey is recognised by its visible shape.

K. and J. ten Cate (1938) have shown that *Octopus* is able to discriminate between a square and a triangle, or between large and small squares, though it is not clear how far size, rather than shape, was reacted to.

There is evidence, therefore, that changes may take place in the nervous system of Cephalopods which modify subsequent reactions. There appears to have been no previous work aimed at discovering the effects of removal of any part of the CNS on this capacity. Indeed there exist only fragmentary observations on the effect of operations on the CNS on the behaviour of these animals. Bert (1867) using *Sepia* and Fredericq (1878) with Octopods, claim that after removal of the entire supra-oesophageal ganglia the animals become wholly passive and show no further spontaneous movements. This was confirmed for Octopods by Phisalix (1892, 1894) who performed a number of operations on the CNS in connection with a search for the chromatophore centre. His observations were mostly concerned with chromatophore changes following operation, but he noted that superficial supraoesophageal lesions do not affect the movements of the animal, while injury to deeper parts produces considerable motor disturbances. Interpretation of all these observations is made difficult by the absence of histological control to show exactly what was removed. In the present work we have attempted to remove, or to interrupt the functions of, only those centres which, as we have seen above, would be expected to constitute the 'highest' portion of the CNS.

OPERATIVE TECHNIQUE

Operation on the supra oesophageal ganglia of *Sepia* is made difficult mainly by the the profuse bleeding which follows opening of the 'cranium.' The animals are anaesthetised with 2 per cent urethane in which they become immobilized in a few minutes. Anaesthesia should be carried to the point at which all the chromatophores become contracted but the respiratory movements of the valves of the mantle still continue. This point is not easy to judge, and some animals were lost through carrying the anaesthesia to a point at which the respiratory movements stopped. Artificial respiration, either by pressing the mantle with the hand, or by direction of a stream of water over the gills is sometimes effective. The animals were wrapped in a damp cloth during the operation, which must be completed

in about fifteen minutes, unless a period of respiration followed by a second anaesthesia is given. No aseptic precautions were taken, but no serious infection was found.

A longitudinal incision is made in the skin between the eyes, and the 'cranium' exposed by severing the muscles attached to its anterior wall. A transverse cut is then made with a fine blade, low down, through the front wall of the cranium, followed by longitudinal upward cuts such as to free a flap of cartilage which can be held up to expose the supraoesophageal ganglia. Profuse bleeding begins as soon as the cranuim is pierced, and in spite of swabbing it is often necessary to operate in a pool of milky bluish blood. The animal may lose several millilitres, apparently without serious ill effects. The bleeding is due to the unavoidable rupture of the intra-cranial venous sinus, but the arteries for the supraoesophageal ganglia and optic lobes run up at the sides of the *back* of the cranium, and are not interfered with by this anterior approach.

The superficial lobes of the supra-oesophageal mass can, with practice, be distinguished externally, and incisions can be made into them as required with a fine sharp cornea knife. The lobes with which we are here concerned are the most superficial and can be easily removed. The whole of lobus verticalis can be sliced off without damage to any other centres. By entering lower down, lobus frontalis superior can be removed, with or without verticalis. Closure of the wound is effected by two or three stitches in the skin. In spite of the damage to the venous sinus post-operative bleeding is very slight, and recovery and survival are good.

The effect of the operative procedure itself on the animal was controlled by making incisions into the skin and cartilage and then closing again without damage to the central nervous system. It is essential to control all lesions by histological examination, since their extent can never be properly determined at operation and autopsy, and secondary changes due to interference with blood supply must be looked for. Post-morten changes in the nervous system are very rapid, and all material was therefore taken immediately after the animals had been killed by decapitation. The eyes were removed, and the whole cranium and central nervous system then fixed in a mixture of 15 parts of 40 per cent neutral formaldehyde and 85 parts of sea water. Any attempt to remove the CNS from the head, or to explore the extent of the lesion at autopsy, leads only to uncertainty as to the extent of the true operative damage.

Material can be kept in formol for several months and is then stained with the modified Cajal's method described by Young (1939). The staining, however, should be undertaken as soon as possible, since with lapse of time the connective tissue is found to stain more strongly, and the nerve fibres less strongly. Good nerve stains can be obtained after one year in the fixative, but pieces kept for five years show only connective tissue.

All material was embedded in celloidin and sectioned serially at 50 or 100μ. This procedure well repays the great labour involved, since it gives a very beautiful picture of the fibres in the neuropil, and also often of their connections with the cells. Degenerating tracts can be identified during the first few days after operation by the rows of granules which they contain. Secondary pathological changes such as those produced by infection or anemia are easily recognised.

EXPERIMENTAL RESULTS

Removal of verticalis complex

Absence of motor defects or forced movements. Table 1 shows the extent of the injury, as revealed by serial sections, in the animals chosen for critical study. In order to map the lesion, the total number of sections (usually sagittal, occasionally transverse) occupied by the verticalis was counted, and divided by 5. The sections corresponding to each of 4 points across the hemisphere was then plotted on to a standard outline of the verticalis and frontalis superior. This outline was obtained from a suitable horizontal section, and is not exactly that seen from above, since the upper part of the verticalis overhangs the l. frontalis superior. A standard outline of a sagittal section was then filled in to show the *maximum* depth of the lesion, which of course did not always extend as deeply as this over the whole area.
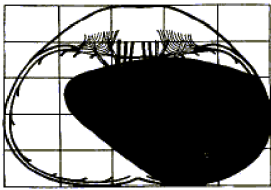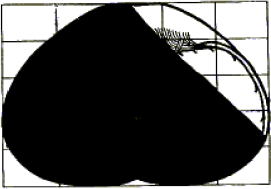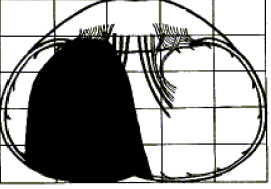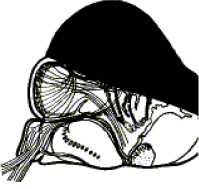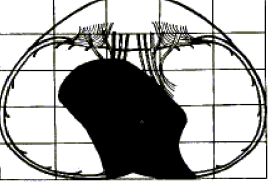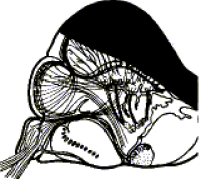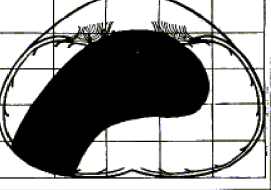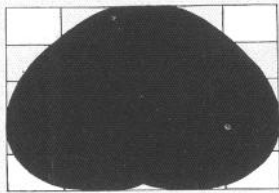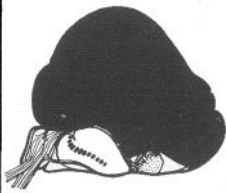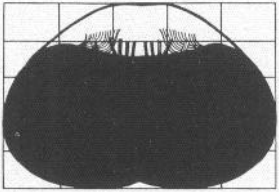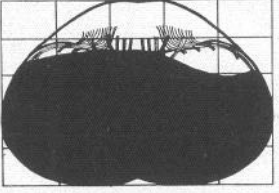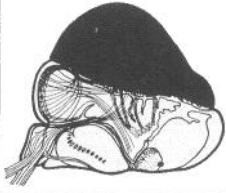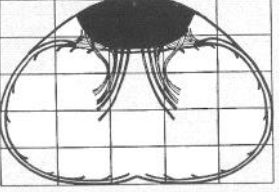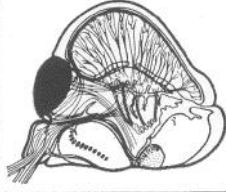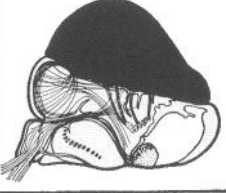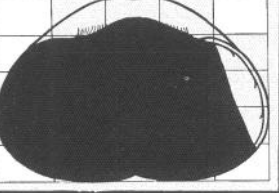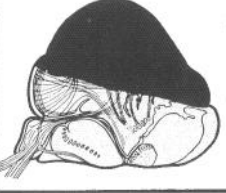
Sepia	Died or Killed	Sur- vival, Days	Surface View of Lesion	Maximum Depth of Lesion
I J	D	2		
I Y	K	3		
L P	K	2		
N Q	K	3		
O A	K	17		
N U	K	2		

Table 1.—Diagrams of supraoesophageal ganglia of Sepia to show the

Sepia	Died or Killed	Survival. Days	Surface View of Lesion	Maximum Depth of Lesion
PA	D	4		
PC	K	9		
PD	K	9		
PE	K	9		
PF	K	6		
PG	D	5		

extent of the lesions inflicted. For method of compilation see p. 503.

Lesions of lobus verticalis and lobus frontalis superior do not produce any obvious effect on the appearance or behaviour of the animal. After complete removal of either or both lobus verticalis and lobus frontalis superior a *Sepia* swims normally with its funnel or fins, and its colour patterns (Holmes 1940) are unaffected in range or intensity. Moreover the animal can steer its way about the tank, avoiding obstacles, and darting away from an approaching stick without any symptoms of blindness, slowness, or any other disability. There are no clear signs of either increased activity (hyperexcitability) or passivity (depression or hypoexcitability). Without some measure of the activity of the animal such as is provided by cage-running in mice, it is difficult to be positive on such points, but the *Sepia* lend themselves very well to observation in a dimly lit glass-sided tank, and any gross disturbance in this respect would certainly be detectable. Indeed after certain operati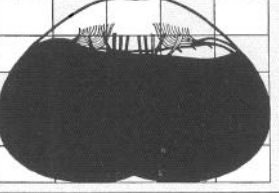ons on the more basal ganglia there is very marked hyperexcitability, the animal dashing recklessly about the tank after the slightest stimulus, or in other cases moving ceaselessly around: but no one of these symptoms is seen after the removal of the verticalis complex. In fact, *after such an operation the animal is quite indistinguishable in its simple behaviour from a normal Sepia*.

Moreover, after unilateral operations, such as those on animals LP and IJ, in which the verticalis was removed on one side only, *there are no forced movements or circling*, either with the fins or the funnel, though such movements are very pronounced after lesions affecting the more basal supraoesophageal centres, especially lobus basalis anterior (Young unpublished). Nor after such unilateral operation is there manifestation of asymmetrical colour patterns, though these again may be produced by deeper lesions.

Careful search for each of the above symptoms was made in every animal shown in Table 1. There is, therefore, every indication that lobus frontalis superior and lobus verticalis do not directly control any simple motor function, nor supply any tonic excitatory or inhibitory influence whose removal produces gross asymmetry in the animal.

Feeding after removal of verticalis complex. Still more surprising than the absence of motor defects after the removal of these centres is the fact that the animals are able to feed in a perfectly normal manner without them. A normal *Sepia*, when hungry and in the presence of a prawn, goes through a complex and well-marked series of reactions (see Holmes 1940). In the first position, which may be termed *attention*, the arms assume a characteristic posture, the two most dorsal being raised almost vertically and the sickle-shaped fifth pair being held out laterally. Meanwhile, waves of darkening pass over the head, and sometimes also over the body, the upraised tentacles being especially dark.

The next stage may be termed that of *approach*. The *Sepia* swims slowly forward towards the prey, following if the latter moves away. If the prawn moves out of sight at this stage the *Sepia* may follow it around a corner, a reaction which we term *hunting* (see below). As it comes nearer to its prey,

the 'tentacles' begin to protrude from the now forwardly pointing arms, and finally when the prawn is within range the reaction of *seizure* takes place, the long tentacles being shot out and the prey caught by the suckers of the expanded tip or 'hand.'

The whole set of movements is carried out in a 'purposeful' manner, each action being modified by circumstances and not following an invariable course. For instance, if the prawn is placed close to the *Sepia* in a clear space it will be rapidly seized, but if some other moving object is included in the field, or if the prawn is moribund or otherwise atypical, the 'attention' pe-
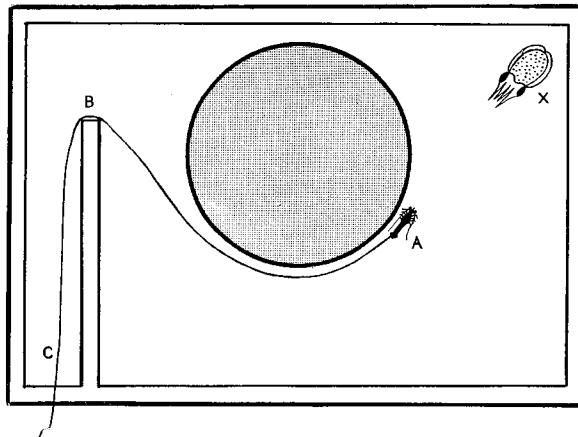
FIG. 4. Arrangement of tank to show capacity of *Sepia* to hunt when its prey passes out of sight, see text.

riod will be prolonged, and the approach very cautious, so that some minutes elapse before seizure is attempted.

After removal of lobus frontalis superior and lobus verticalis, a *Sepia* can attack and eat its prey in a perfectly normal manner, *provided that the food-object remains in the visual field until captured.* When a prawn was placed in the tank, 'attention', 'approach', and 'seizure' were seen to take place in all the animals in Table 1 in a manner indistinguishable from normal, providing that no 'hunting' was required. These centres are therefore not an essential part of the mechanism by which the shape of the food-object is recognised, or the hunger drive operated.

There is, however, some effect of the removal of these centres on feeding, since the animals often refused food for some days immediately after the operation, or, as in the case of animal PE, showed 'attention' but made no attempt at seizure of the food. No such changes were seen after a control procedure in which the cranium was opened but no damage inflicted on the CNS (see Fig. 5).

Inability to hunt after removal of verticalis complex. In order to investigate the capacity of *Sepia* to hunt food which disappears out of its sight, a black

thread was tied to the tail of the prawns, and the tank provided with a simple maze in the form of an enamel plate stretching three quarters of the way across the tank, and an enamel bucket (Fig. 4). The prawn was placed in the tank at A, in such a way that it could be seen by the *Sepia*, which was at rest in the corner at X.

If necessary the *Sepia* was steered to this point before each experiment, but this gave little trouble since nearly all animals chose this corner as a permanent point of rest during the day, always returning to it after excursion round the tank or capture of the prawn at the end of a trial. When the *Sepia* showed 'attention' and began to follow the prawn, the latter was withdrawn out of the visual field behind the bucket and allowed to rest at the corner B. If the *Sepia* followed round the bucket until it could again see the prawn, the latter was further withdrawn behind the enamel plate to C, where the *Sepia*, if it had followed round the corner, was allowed to seize and eat the prey. The presence of the black thread did not appear to interfere with 'attention' or feeding in any way.

The arrangement therefore makes it necessary for the *Sepia* twice to follow its prey after the latter has passed out of its sight, and the experiment thus tests the capacity of the animal to make a response to a situation in which no directly stimulating object is in the visual field. Put in another way it tests whether the animal is able to retain the association of a particular locality with the food-object which is no longer present there, and to use this association for its hunting. A great advantage of this experiment is that it investigates a type of response likely to be of use to the animal in its natural surroundings among the rocks, and is therefore perhaps of greater interest than discovery of the capacity of the animal to discriminate triangles from squares, or to learn the problems discussed later (p. 26).

When tested in this way, a normal *Sepia*, provided it is hungry and has become accustomed to the tank by living in it for a day or so, shows 'attention' as soon as the prawn appears, advances towards it, follows round the bucket and the edge of the plate, and eats it at C. The following is often rapid and the whole reaction accomplished within a minute or less. At other times the animal waits for as much as two minutes before gradually turning the corners. Occasionally, if the prawn is withdrawn very soon after having been placed at A, the *Sepia* does not follow round the bucket, but retreats again to its corner.

If the cuttlefish has been sated it usually gives no sign even of attention, much less of following, or it may give attention without following. The number of prawns which will be taken daily varies considerably; often it is only one, sometimes two or three. A hungry animal which has just finished a prawn will often immediately take another, perhaps even a third, but thereafter shows no further attention to prawns for some hours. If one prawn only is given daily, normal animals give the hunting reaction with complete regularity at each day's presentation.

After removal of lobus verticalis, however, the behaviour is very different. The *Sepia* shows attention to the prawn, and advances towards it, but

when the latter is withdrawn out of sight, *the cuttlefish never hunts it,* even round the edge of the bucket. As will be seen from Fig. 5, this was tested many times on the operated animals. Every device was used to encourage the animals to follow and hunt, the prawn being withdrawn as slowly as was possible without its being captured by the *Sepia.* In every case, however, when the prawn disappeared from its field of view, the *Sepia,* after pausing for few seconds, shot back to its corner as if baffled. The course of the experiment may be shown by a typical case (see Fig. 5), *Sepia OA.* Before operation the animal was given two trials on each of two successive
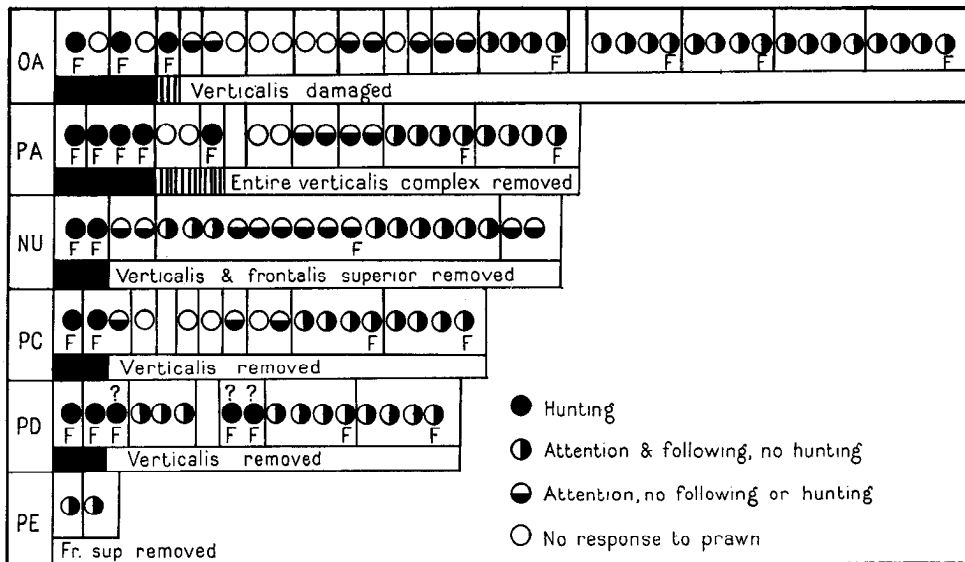
FIG. 5. Failure of *Sepia* to hunt after injury to the verticalis complex. Each spot indicates a test whose result is indicated by the key. The vertical lines indicate days. The black area below each row of spots shows the period before operation of the animal, the vertically hatched area the period after a control operation, and the area with the lettering the period after the operation as named. The *Sepia* was allowed to eat the prawn in the trials marked F, but had no other food throughout the experiment.

days, giving the full hunting reaction on the first trial of each day, but showing no 'attention' at the second trials. On the third day a control operation was made, the skin being incised and the cranium opened, but the wound then closed without any injury to the supra-oesophageal ganglia. After recovery from anaesthesia a further trial was made and a hunting reaction again obtained. On the fourth day the wound was opened again and a lesion made which was presumed to cut off the whole lobus verticalis. For thirteen successive trials during the succeeding 8 days, the animal either took no interest in the prawn, or showed 'attention' without following. Then followed 20 trials during a further 6 days, at each of which there was attention and following of the prawn, but in which the animal was unable to perform the hunting reaction, that is to say to follow when its prey moved out of

sight. The procedure on each of these days was to test the animal 4 times, twice in the morning and twice in the evening, by drawing the prawn away from it, so that each day's performance consists of four tests of the ability of the cuttlefish to hunt. On each day after the four tests, the *Sepia* was allowed to catch and eat a prawn. As will be seen from Table 1, subsequent sections showed that in this animal sufficient of lobus verticalis had been removed to interrupt tractus verticalis-frontalis superior on both sides, though large amounts of the lateral part of verticalis were intact, as was most of frontalis superior.

As will be seen from Fig. 5, essentially similar results were obtained with animals NU, PA and PC when tested in the same way. Two further animals, PD and PE, were tested by a somewhat different, and as it proved less satisfactory, technique, using the tank designed for the learning experiments described in the next section. Each animal was confined in a separate runway (see Fig. 6) one end of which was closed by a sliding wooden door, which when opened revealed the prawn. As the *Sepia* moved up towards the door the prawn was removed sideways out of view, and a positive hunting reaction was recorded when the *Sepia* continued onwards through the doorway. The defect of the device was that the runway was too short, so that if the *Sepia* moved fast it was apt to be carried through by its own momentum. Moreover it was difficult to withdraw the prawn fast enough to take it out of the view of the *Sepia* for more than a short time. In spite of this difficulty the results are included, since animal PD 10 times failed after operation to make the very simple hunting reaction necessary to capture its prey in this device. At three trials it did pass through the doorway, but in each of these cases it came up the runway very fast, and probably kept the prawn in view throughout.
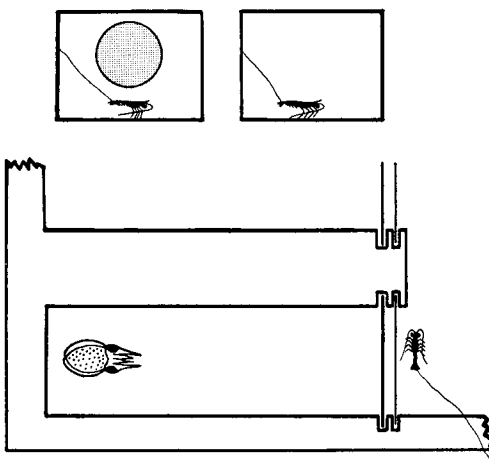

FIG. 6. Arrangement for testing reaction of *Sepia* to a prawn behind glass. Above is shown the end of the tank as it would appear with and without the glass and white spot.

Sepia PE was an animal previously tested and operated in connection with the learning experiments to be described in the next section. Accordingly no record was made of its ability to perform a hunting reaction before operation; however, every normal animal tested proved able to hunt. Tested in the runway *after* operation, it gave 2 successive trials in which attention and following of the moving prawn took place, but without the ability to perform the hunting reaction of coming through the door. These 2 animals,

therefore, provide further confirmation of the result shown by the other four, namely that following of food which has been moved out of sight is not possible after injury to the verticalis complex.

Experiments on learning in Sepia

A further series of experiments was designed to study the modification of behaviour as a result of experience, and the relation of this power to the verticalis complex.

Inhibition of 'seizure' reaction   It was noticed that if a glass jar containing a prawn was placed in a tank of *Sepia*, the animals at first attempted to seize the prawn, shooting their tentacles repeatedly against the glass. Gradually the attacks became less frequent, and finally the prawn was completely ignored. Clearly some change takes place in the nervous system such that a situation which at first elicits the attacks on the prawn later fails to do so. This inhibition of feeding reaction was further studied by keeping the animals in a tank provided with running seawater, divided by means of longitudinal partitions into a number of runways, each closed by a sliding wooden door (Fig. 6). One animal was confined in each runway for the duration of the experiment. The opening of the wooden door gave the animal access to an open space in the tank. In addition, slots were provided at the open end of each runway, so that a sheet of glass, as well as the wooden door, could be placed across the opening.

The animals were placed in the runways and allowed several hours in order to become used to the tank. At the beginning of an experiment the glass plate was placed in position across the end of the runway with a prawn behind it, the wooden door being kept closed. The door was then opened and the *Sepia* in the runway allowed to attempt to take the prawn, which it did repeatedly, shooting its tentacles violently against the glass plate.

It was found in the course of an experiment that this ejection of the tentacles became less frequent. The frequency of ejection was thus used as an index of the state of the animal, and, taking zero as the time of opening the door, the time (in seconds) at which each 'shot' was made was recorded. The experiment was ended when 3 minutes passed without any shot being made. The animal was then left undisturbed in the tank for a number of hours and then tested again with the same technique, the time of each shot being again taken until none had occurred in 3 min.

The animals were not fed throughout the experiment, which lasted at the most for ten days. They are able to starve for such long periods without showing obvious debility. In order to follow quantitatively the change which is occurring in the state of the nervous system as the learning proceeds, the number of shots per two minutes was plotted against time as shown in Fig. 7. With each of the animals tested it was found that the rate of tentacle ejection fell off from a very high value at the beginning of the first test period, until after 20–30 min. the criterion of no shots per 3 min. was reached. The curve is not smooth, but shows several minor peaks.

When the test was repeated after intervals up to eighteen hours, the animals usually made some shots at the glass, but *always less than in the first experiment*. The highest frequency of shots was often reached some minutes after the beginning of the test, and thereafter rapidly declined, the 3-minute criterion being reached much sooner than in the original test. Moreover the time taken to reach this criterion tended to become shorter at each successive test, the fall in this value showing a more or less regular 'learning curve.' Thus not only does the state of the nervous system change during the course of one test: the animal 'learns' to inhibit its seizure reaction: but also this
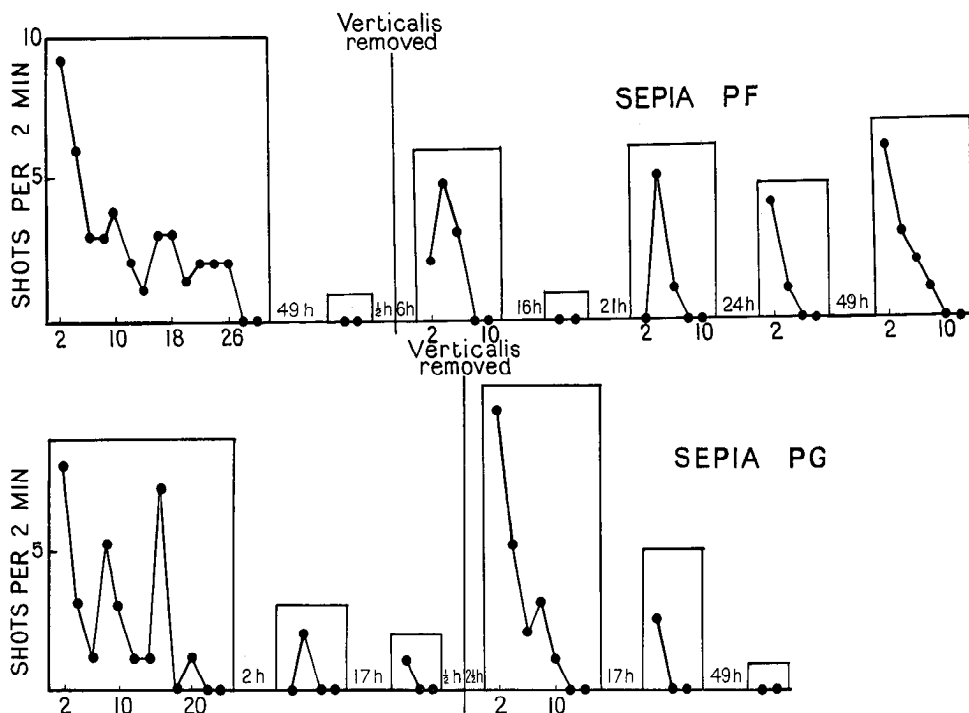
FIG. 7. Graphs showing the number of shots made at the glass per 2 min., before and after injury to the verticalis complex. The time scale for each test is in minutes and the periods between the tests are given in hours.

learning is carried over a period of at least 18 hours. But in most cases the change of state in the CNS, whatever it may be, which enforces this inhibition is partly reversed after such an interval. The animals have partly 'forgotten,' but quickly learn again.

Details of the maximum period of retention were not further investigated since the purpose of the experiment was to test the effect of the removal of the verticalis complex upon learning. The results are not wholly consistent. Sepia PG showed the clearest result. When tested after the operation it showed a higher frequency of tentacle ejection than at the very first test.

This is very remarkable since only 3 hours elapsed between this test and the last before operation, whereas the inhibition was not lost in the much longer periods between the pre-operational tests. There can be no doubt that the operation has produced a marked effect on the learning. However, the experiment is uncontrolled since the effect of anaesthesia alone on the learning was not investigated. Much more significant is the fact that after this initial high value the ejection frequency fell off sharply. Therefore, even after an operation in which, as Table 1 shows, very nearly the whole of the lobus verticalis had been removed, the animal was able to learn to inhibit the seizure reaction. Moreover it learns to do so more rapidly than in the first test, that is to say some part of the changed state of the CNS is carried over in spite of the operation. It is therefore quite clear that the change of state involved in this particular act of learning does not occur only in the verticalis complex.

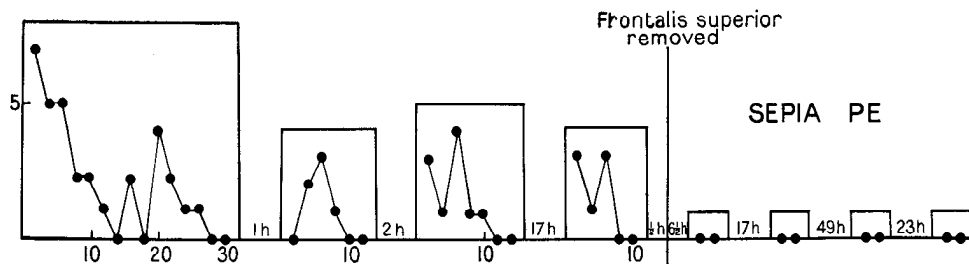Sepia PF showed similar behaviour in that considerable traces of the

FIG. 8. As for Fig. 7. In this case the *Sepia* made no further shots at the glass after operation.

learning persisted over the operation, without, however any very high post-operative frequency of tentacle ejection.

Sepia PE gave a most curious result in that during five post-operational tests it at no time shot its tentacles at the glass. At each test the *Sepia* showed attention to the prawn throughout the experimental period, thrusting its head against the glass and moving excitedly up and down the tank, but never once were the tentacles ejected. In this case the operation, far from causing the animal to forget the learned inhibition, appeared to have made this inhibition more profound. It will be remembered that in the experiments detailed on p. 509, the feeding reactions were often affected during the period immediately after operation. But in these cases attention to the prawn was rare, whereas here there is clear evidence of attention, but a curiously accentuated inhibition of seizure. The operation performed in this case was the removal of lobus frontalis superior, not verticalis itself. It acts as a warning against treating all lesions of the verticalis complex as if they were equivalent, but in the absence of further evidence it is impossible at present to pursue further the questions which it raises.

In spite of the differences between the behaviour of these 3 animals, they

agree in showing that the change of state involved in learning to inhibit the ejection of the tentacles does not occur in the verticalis complex, since considerable traces of the learned state may persist after removal of this complex, and subsequent learning is at least as rapid as that before removal. The experiments indicate however that the verticalis complex may have some influence on the type of learning studied even though its presence is not necessary for the learning to take place.

Discrimination. The reaction of tentacle ejection was also used in a study of the ability of *Sepia* to learn a discrimination problem. The animals were presented with a prawn behind a glass plate marked with a white circle, and then learned not to eject the tentacles at this, while continuing normal ejection at a prawn presented without a glass plate. The discrimination was thus between 'prawn' as a food-object, and 'prawn plus white circle' as a non-food-object.

Apparatus and technique. The apparatus used in this experiment was a wooden tank divided into runways as in the case of the tank used in the study of tentacle ejection inhibition alone (Fig. 6). As the discrimination presents a much harder problem for the *Sepia* than the reactions previously described, and the experiment was consequently much longer, each runway was provided with a separate sea-water supply, and the animals kept permanently in this space for several weeks remained very healthy.

Every day each animal was given a group of 4 trials. These trials were of two types: (i) '*glass*' *trials* in which the prawn was presented behind a glass plate bearing just above its centre a painted white circle two inches in diameter; (ii) '*feeding*' *trials* in which the prawn was presented alone.

The technique of presentation of the prawn in the case of both types of trial was the same as that described for the experiments above. The daily group of trials was made up as follows: (i) *Three* successive 'glass' trials; (ii) *The fourth* and last trial of the day, a feeding' trial, in which no glass was used, and the *Sepia* allowed to reach and seize the prawn.

This grouping of trials was evolved to meet a practical difficulty, that of giving a number of trials on the same day. In the normal manner, an animal being trained in a discrimination problem would be given a number of trials of the two different types (*e.g.* in this case 'glass' and 'feeding' trials) arranged in a purely random order. However it was found in preliminary experiments that it was undesirable to feed the *Sepia* with more than one prawn a day. Thus if a 'feeding' trial preceded a 'glass' trial on any one day, the *Sepia* was unlikely to take any interest in the prawn at the second trial. A random arrangement of 'feeding' and 'glass' trials would thus limit the experiment to one trial per day. An alternate arrangement of 'glass' and 'feeding' trials was avoided, since it might possibly be objected that the animal was learning to respond to very alternate trial rather than to 'prawn' versus 'prawn+white circle'. As it is very unlikely that the CNS of *Sepia* would enable discrimination of every 4th trial from the rest, solely by virtue of its position in the series, the above arrangement was adopted. This gave the convenience of 4 trials per day, combined with the advantage of not feeding the animal until the last trial of the day.

In the case of 'glass' trials two indices of the state of the animal were taken, the time in seconds from the opening of the wooden door to the first

ejection of the tentacles, and the number of shots made in the first two minutes following this first shot. It was found that the time to the first shot lengthened and the number of shots made in the extra period declined during the course of the experiment. The discrimination was regarded as learnt when in each of the 6 consecutive 'glass' trials (*i.e.*, the trials of 2 successive days) no ejection was made in the first five minutes of experiment, while in the 2 accompanying 'feeding' trials positive responses (*i.e.*, feeding) were recorded. The number of shots made at the glass each day during the 2 min. is thus an index of the extent to which learning has taken place. When plotted against time the number of shots declines with the irregularity typical of most learning curves. When the total number of shots in three successive days of experiment are plotted, the general slopes of the curves appear, and are seen to be similar for the three animals investigated (Fig. 9).

FIG. 9. Graph of course of learning not to shoot at prawn behind a glass plate on which there is a white circle. The ordinate shows the number of shots made at the glass(*i.e.*, 'mistakes') during successive periods of 3 days.

Figure 10 is a diagram illustrating the progressive changes in the behaviour of the three animals during the course of this learning. At the beginning of the experiment 'glass' trials were invariably accompanied by shooting, but quite early, with all three animals, there appeared occasional trials in which there was attention or approach to the glass without any tentacle ejection. As the experiment proceeded, such trials, involving only attention or approach, grew more frequent, as did trials in which the *Sepia* ignored the prawn entirely, though continuing to seize the prawn in the accompanying 'feeding' trials. Finally, the criterion of learning adopted was reached. All 3 animals proved capable,

FIG. 10. Diagram to show the gradual failure of *Sepia* to respond to a prawn shown behind a glass plate provided with a white circle. For each animal the upper row of spots (G) shows the 'glass' trials and the lower row (F) the 'feeding' trials, there being three of the former and one of the latter daily. Vertical lines mark the days. During the experiment each animal gives progressively fewer trials at which there is attention or shooting if the white circle is showing, while continuing to shoot when it is absent.

therefore, of making a discrimination between 'prawn' and 'prawn +white circle' as objects of different significance. The criterion adopted was reached in the case of Sepia NJ after 38 'glass' trials, and in the cases of NK and PB, after 55 and 48 trials respectively. The discrimination is of a similar sort to that performed by the 2 *Octopus* of K. and J. ten Cate (1938).

A question arises concerning the importance of tactile influences in the setting up of this discrimination. In some of the trials in which there was attention and approach but no seizure, the animal 'felt' the glass with its tentacles, and of course, during the abortive shooting of the tentacles in 'glass' trials, the glass was struck violently by the ejected tentacles, so that tactile, possibly 'painful', stimulation must have been involved. Whatever tactual stimuli are involved in the learning, when the final criterion was reached, the *Sepia* remained immobile at the end of their tanks in the trials when 'prawn +white circle' was presented, a situation in which the *Sepia* has of course, no tactual relation with the glass plate.

The only further difference, other than optical, between the two situations in which positive and negative responses were given, is that in the 'glass' trials possible chemical influences emanating from the prawn are excluded. Although chemoreceptors are certainly present in Cephalopods, there is no evidence that they function as distance receptors. Indeed the fact that at the beginning of the experiment the *Sepia does attack* the prawn in 'glass' trials shows that the distance receptors involved are the eyes. Thus there is every reason to believe that *Sepia* can make a discrimination between the two visual situations.

Unfortunately the experiments were interrupted before we could make tests of the retention of this type of learning or of the effect upon it of the removal of the verticalis complex. However these experiments show for the first time that *Sepia* is capable of learning to make such a discrimination, and indeed that it lends itself well to this type of experiment.

DISCUSSION

From all of these experiments it is clear that changes of state may occur in the nervous system of *Sepia*, so that following certain situations the reaction capacities are altered. After a prawn has disappeared round a corner that corner exerts an attraction which it did not possess before. After a *Sepia* has repeatedly and vainly shot its tentacles at a prawn behind a glass plate, the futile reaction ceases to be given. After training, a *Sepia* will not attack a prawn if a white circle is also present, but only when the prawn alone appears.

Such modifications of behaviour are all examples of a process which may be called learning, and they show capacities which are likely to be extremely valuable to the animals in meeting their daily needs. This is especially clear in the case of the hunting reaction. A search for prawns among rocks would be difficult for a *Sepia* which was unable to follow its prey out of sight. The other situations studied, though they are never likely to be met with in the

life of the animal in this form, yet show capacities for modification by experience which could be applied to many situations.

These experiments, then, give us further knowledge about the behaviour and mode of life of the cuttlefish. But the main purpose of the investigation was to attempt to discover something of the nature of the change which takes place in the nervous system during the process of learning. All hypotheses hitherto suggested about this change have proved either inadequate to cover the facts or inacceptable to the physiologist (see Lashley, 1934, for summary). The particular hypothesis upon which the present work has been based was that the change taking place during learning consists in the setting-up of self-re-exciting activities which so facilitate the effects of impulses from sensory sources as to make them able to produce a response which they could not elicit before the training. Such a theory certainly allows us to understand some of the aspects of learning. For instance, once the activities have been set up, they might well affect large masses of nervous tissue, so that facilitation would be available for impulses from sources other than the peripheral receptors originally used in learning. Similarly, the degree or amount of learning, as expressed by the learning curve, would depend upon the number of neurons activated in a particular cyclical manner, and when large numbers are set in action at once, sudden drops in the learning curve, 'insight solutions' and the like are produced. Further, a possible basis is provided for the observation that the rate of learning depends on the quantity of tissue present (Lashley 1934 atc.).

In its present form, however, the theory does not give a clear view of the mechanism 'by which a response to a ratio of intensities is brought about' (Lashley, 1937). Thus during the present investigation it has been shown that there is some mechanism in the optic lobes by which a *Sepia* reacts to a prawn as a food-object, or by which the reaction of ejection is inhibited when the prawn is behind a glass plate. The element in these or any other discrimination reactions which is so difficult to understand is that they depend on giving a particular set of reactions to specific patterns of excitation received *anywhere* on the sensory surface. Thus we have to imagine that at least a large portion of the optic lobe is able to elicit a feeding reaction whenever the prawn shape is represented in it, even though individual elements are very variously stimulated at successive presentations.

The only contribution we can bring to this problem is the demonstration that discrimination of this type can certainly be performed in the optic lobes of *Sepia*, without the participation of the verticalis complex. After removal of the latter the cuttlefish not only still shows specific reactions to food-objects, but is able to reverse this discrimination, learning to inhibit the ejection of the tentacles at a prawn behind a glass plate.

However, it seems that the power to form the association involved in the hunting reaction is dependent on the integrity of the verticalis complex, and it is reasonable to suppose that this effect depends in some way on the re-activation of the optic lobes through the cyclical pathways shown in Fig. 1.

Thus it may be that the presence of the food object, in addition to eliciting the feeding reaction, also sets up processes in the verticalis complex which so influence the optic lobes as to cause associated configurations, such as the corner round which the prawn has disappeared to elicit following reactions which they alone could not produce. Since we know nothing of the method by which one configuration rather than another produces its effect it is not profitable at present to speculate further on this baffling theme.

The hypothesis of self-re-exciting chains, in the simple form of the inter-action of lobes considered above, is clearly inadequate to meet all the requirements of learning situations even as simple as those here studied, which demand a knowledge of how masses of tissue, such as the optic lobes, change their state so as to become responsive to certain configurations projected upon them. It is by no means excluded that self-re-exciting activities within the lobes play a central part in such changes. For further advance we require more information about the structure and mode of activity of the centres in which such changes take place. There is everything to be gained from study of these centres in as many animal types as possible.

The present study has at least shown something of the capacities of *Sepia* and of the activities of its higher nervous centres. Perhaps the most out-standing point is that removal of the verticalis complex not only does not produce any gross motor abnormality but does not even prevent discrimination, or feeding, though it may affect these processes indirectly, and certainly makes the hunting reaction impossible. The optic lobes alone, as we have come to realise ever more fully as the investigation proceeded, are able, with their relatively uniform, if complex, structure to mediate by themselves many of the more elaborate types of behaviour.

SUMMARY

1. Four types of centre are recognised in the CNS of *Sepia*, (a) *lower motor centres*, in the sub-oesophageal ganglia, comparable to the spinal cord of mammals; (b) *higher motor centres* at the base of the supra-oesophageal ganglia; (c) *primary sensory centres*, such as the optic lobes, and (d) *correlation centres*, occupying the dorsal region of the supra-oesophageal ganglia.

2. The correlation centres, the verticalis complex, allow opportunity for interaction between impulses from various afferent sources, and send tracts to the higher motor centres and to the optic lobes.

3. Faradic stimulation of the lobes of the verticalis complex produces no visible movements; they are 'silent areas.'

4. After complete removal of the verticalis complex the behaviour of a *Sepia* shows no superficial abnormalities. The animal is not blind and can steer and move around as if normal. There is no evidence of either hyper-excitability or depression.

5. After unilateral removal of these centres there are no forced or circling movements, or colour asymmetries, though such are found after injuries affecting the more basal centres of the supra-oesophageal ganglia.

6. After complete removal of the verticalis complex a *Sepia* shows the reaction of attention to a prawn and advances towards it, seizes it and eats it in a manner indistinguishable from normal.

7. A normal *Sepia* is able to hunt, that is to continue to follow a prawn which passes out of its sight round a corner.

8. After removal of the verticalis complex *Sepia* is unable to hunt in this manner, and can then catch its prey only if the latter remains within the visual field.

9. If a normal *Sepia* is presented with a prawn behind a sheet of glass it will shoot its tentacles at the glass, but with a frequency which steadily diminishes. When tested after intervals as long as eighteen hours, considerable traces of this changed state are still evident, the tentacles not being shot as frequently as in the first test, and complete inhibition being more rapidly reached.

10. Removal of the verticalis complex disturbs this state of learned inhibition in various ways, but distinct traces of a previously learned inhibition are seen after removal, and relearning continues to be at least as rapid as the initial learning. The change of state concerned in this learned inhibition does not therefore necessarily involve the presence of the verticalis complex.

11. Three *Sepia* were trained not to eject the tentacles at a prawn showing behind a glass plate on which a white circle was painted, while continuing to shoot at prawns not accompanied by glass and circle.

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