

The functional organization of the brain of the cuttlefish *Sepia officinalis*

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(Communicated by J. Z. Young, F.R.S.—Received 15 June 1960—
Revised 30 August 1960)

[Plates 20 to 22]

The functional organization of the brain of *Sepia* has been investigated by electrical stimulation. As a result several new divisions of the brain have been made. The pedal ganglion has been shown to consist of four parts: (1) the anterior chromatophore lobes innervating the skin and muscles of the anterior part of the head and arms; (2) the anterior pedal lobe innervating the arms and tentacles; (3) the posterior pedal lobe innervating the funnel, collar and retractor muscles of the head; (4) the lateral pedal lobes innervating the muscles of the eyes and tissues of the orbits. The palliovisceral (or visceral) ganglion, apart from the magnocellular lobe demonstrated by Young (1939), is shown here to consist of (1) a central palliovisceral lobe innervating the mantle, funnel and viscera; (2) a pair of lobes innervating the muscles of the fins; (3) a pair of posterior chromatophore lobes innervating the muscles of the chromatophores and skin of the mantle, fin and back of the head; (4) a pair of vasomotor lobes. Because of these new divisions the three main groupings of the suboesophageal neural tissue are now referred to as the anterior, middle and posterior suboesophageal masses corresponding to the old brachial, pedal and palliovisceral divisions.

The suboesophageal centres are classified as lower motor centres and intermediate motor centres, depending on the kind of response they give to electrical stimulation and their peripheral connexions. In the supraoesophageal lobes, higher motor centres and silent areas are recognized. The silent areas include the vertical, superior frontal, subvertical, precommissural and dorsal basal lobes. Of the higher motor centres the anterior basal lobe is primarily concerned with the positioning of the head, arms and eyes, particularly during movements involving changes in direction while swimming. Such manoeuvres are brought about by the anterior basal lobe control over the fins and position of the funnel. The posterior basal lobe is here shown to consist of six main divisions: (1) the subvertical lobe; (2) the dorsal basal lobes; (3) the precommissural lobe; (4) the medial basal lobe; (5) the lateral basal lobe; (6) the interbasal lobe. The medial, lateral and interbasal lobes are higher motor centres. The lateral and medial basal lobes control movements of the chromatophores and skin; the medial basal lobe controls swimming, breathing, fin movements and various visceral functions. The interbasal lobe controls the movements of the tentacles.

The optic nerves and the optic lobes, at their periphery, are electrically inexcitable. Electrical stimulation of the centre of the optic lobes evokes all the responses that can be obtained from the other higher motor centres.

The results are discussed in terms of Sanders & Young's (1940) physiological classification of the brain. A further category intermediate motor centre is recognized. Summary lists of the responses of each lobe are given on pages 516, 520, 525.

1. INTRODUCTION

The object of this paper is to describe the functioning of the main parts of the brain of *Sepia* as revealed by electrical stimulation. The work of previous authors is described where the results of stimulation of each lobe are reported. The results have necessitated some alterations in the nomenclature of the parts of the brain. To avoid confusion, therefore, some of the results are anticipated by beginning with a general account of the anatomy of the brain. An account of the behaviour of the cuttlefish has been given by Boycott (1958). Other observations are to be

found in Grimpe (1928), Bott (1938), Tompsett (1939), L. Tinbergen (1939), and Holmes (1940). D. P. Wilson (1946, 1947, 1951) gives excellent illustrations of his observations.

2. ANATOMY OF THE CUTTLEFISH BRAIN

Dietl (1878) provided the main basis for the terminology of the cephalopod brain, and Hillig (1912) gave a general description of the brain and peripheral nervous system of *Sepia*. Despite these two papers and numerous others from the Leipzig school on other cephalopods (for summary see Hanström 1928), there was little in the way of further anatomical analysis until Thore (1939) recognized new regions and renamed old ones in a variety of cephalopods. The terminology used here is, however, basically that of Dietl (1878) and Hillig (1912).

The brain of *Sepia* is situated between the eyes and is enclosed in a cartilaginous cranium. The oesophagus runs through the brain, dividing it into supraoesophageal and suboesophageal masses (figure 1, plate 20). However, as Young (1939) discovered, there is at least one perioesophageal lobe—the magnocellular lobe (figure 3, plate 21). On either side of the perioesophageal parts of the brain are large optic lobes joined to the supraoesophageal mass by short optic tracts. On each optic tract there are three structures (figure 2, plate 20), the optic gland, the olfactory lobe and the peduncle lobe (Boycott & Young 1956).

At the top of the supraoesophageal mass there are three lobes, named from in front backwards the inferior frontal, superior frontal and vertical lobes (figure 4, plate 21) Dietl (1878). Underneath the vertical lobe is the subvertical lobe, and immediately under that the precommissural lobe, so called because it lies in front of the ventral optic commissure (figure 4, plate 21; figure 5, plate 22). The remainder of the supraoesophageal mass consists of the anterior and posterior basal lobes. The posterior basal lobe of Dietl (1878) is used now only as a general term to include regions shown here to have different functions as well as being distinguishable anatomically. It includes the precommissural and subvertical lobes mentioned above and four other lobes: (1) the dorsal basal lobe, which forms the upper part of the posterior wall of the supraoesophageal mass and lies underneath the vertical lobe but behind the subvertical lobe (figure 4, plate 21). (2) The medial basal lobe, which lies immediately under the dorsal basal lobe (figure 4, plate 21; figure 5, plate 22). (3) The lateral basal lobes lying one on either side of the medial basal lobe (figure 5, plate 22). (4) The interbasal lobes which lie one on either side, between the anterior basal lobe and the medial and lateral basal lobes (figure 6, plate 22).

The suboesophageal mass is divided into three regions, the anterior, middle and posterior suboesophageal masses. These divisions correspond to the old brachial, pedal and palliovisceral (or visceral) ganglia. This new terminology is made necessary by the recognition, as a result of the present experiments, of more parts to the suboesophageal centres than have previously been described. The anterior suboesophageal mass includes only the brachial lobe in decapods. The middle suboesophageal mass is here divided into anterior pedal, posterior pedal and lateral pedal lobes, with an anterior chromatophore lobe in the wall of either side of the anterior pedal lobe. The division into anterior and posterior pedal lobes is marked by the fibres

dorsal

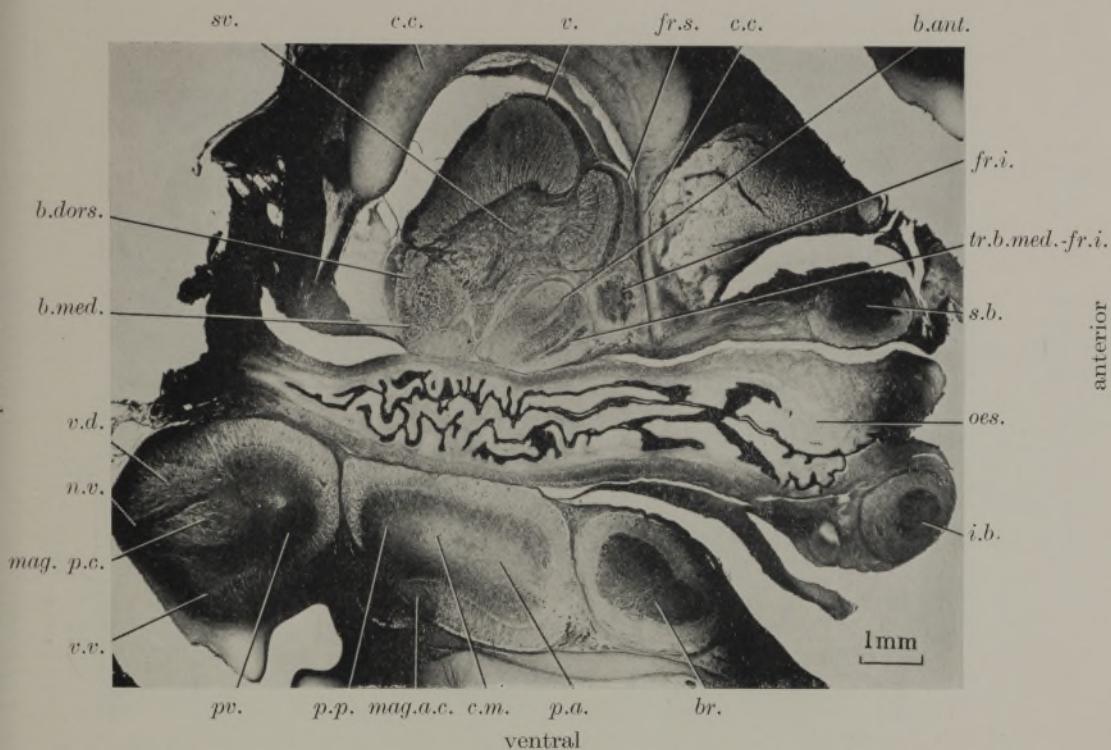


FIGURE 1. Sagittal section through the brain near the midline. This and all other figures are of brains of *Sepia* stained by a Cajal method. The visceral nerve (*n.v.*) has two roots, one above and one below the posterior magnocellular commissure (*mag.p.c.*). For summary of abbreviations see back of plate 22.

dorsal

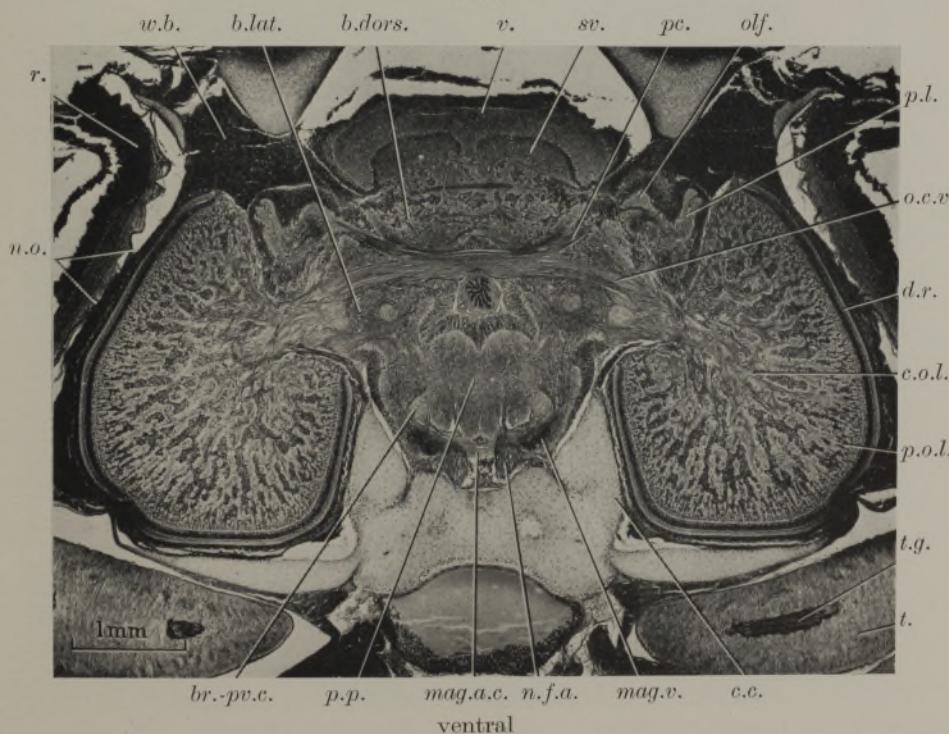


FIGURE 2. Transverse section through the brain of a young specimen at the level of the anterior magnocellular (*mag.a.c.*), ventral optic (*o.c.v.*) and peduncle commissures (*pc.*).

(Facing p. 504)

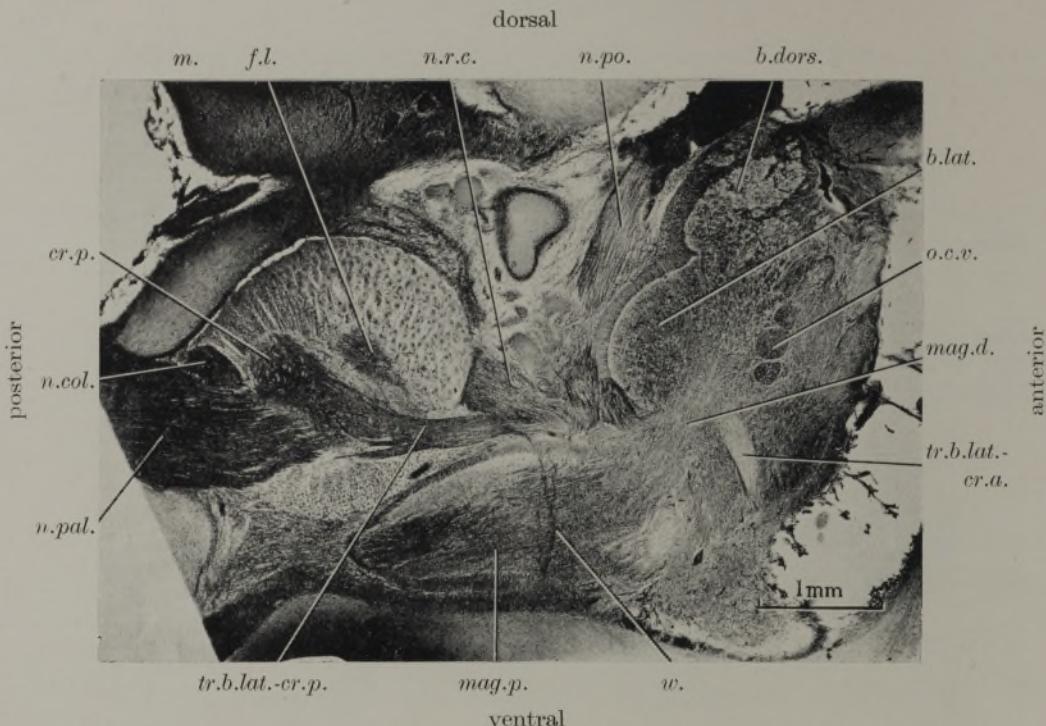


FIGURE 3. Lateral sagittal section showing the relationships of the lobes at the side of the brain. The fin lobe (*f.l.*) lies more medial than the posterior chromatophore lobe (*cr.p.*) so that only the outer side of it is cut through.

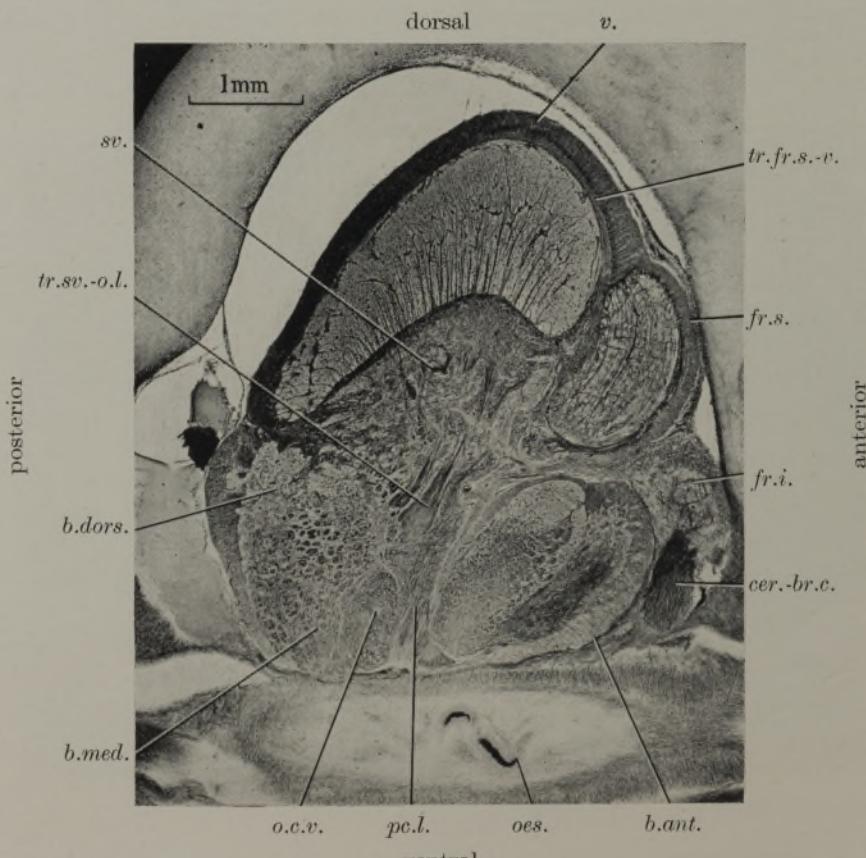


FIGURE 4. Sagittal section of the supraoesophageal lobes only. The section is just to one side of the midline.

anterior

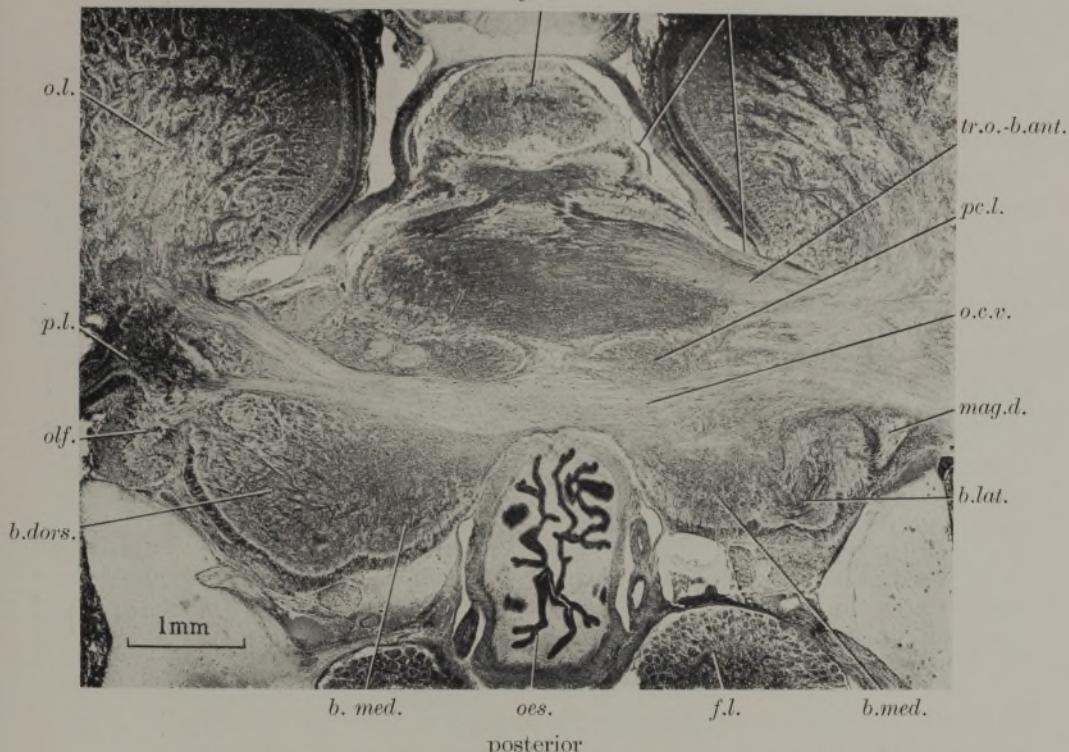
*fr.i.**b.ant.*

FIGURE 5. Oblique horizontal section through the supraoesophageal lobes. The section is slightly more dorsal on the left than the right and slopes from front to back. Thus on the left a portion of the dorsal basal lobe with its close connexions with the olfactory lobe is shown, while on the right the top of the lateral basal lobe is visible.

*tr.o.-b.ant.**b.int.**tr.b.lat.-cr.a.**mag.d.*

FIGURE 6. Higher power of the same series as figure 5, but of a section slightly more towards the suboesophageal lobes. The section shows how, at the side of the brain, the anterior basal, medial basal, lateral basal and precommissural lobes are all joined in a region here called the interbasal lobe.

SUMMARY OF ABBREVIATIONS FOR PLATES 20 TO 22

<i>b.ant.</i> , anterior basal lobe	<i>oes.</i> , oesophagus
<i>b.dors.</i> , dorsal basal lobe	<i>olf.</i> , olfactory lobe
<i>b.int.</i> , interbasal lobe	<i>o.l.</i> , optic lobe
<i>b.lat.</i> , lateral basal lobe	<i>o.c.v.</i> , ventral optic commissure
<i>b.med.</i> , medial basal lobe	
<i>br.</i> , brachial lobe	<i>pc.</i> , peduncle commissure
<i>br.-pv.c.</i> , brachio-palliovisceral connective	<i>pv.</i> , palliovisceral lobe
<i>c.c.</i> , cranial cartilage	<i>p.a.</i> , anterior pedal lobe
<i>c.m.</i> , middle pedal commissure	<i>p.l.</i> , peduncle lobe
<i>c.o.l.</i> , centre of optic lobe	<i>p.o.l.</i> , periphery of the optic lobe
<i>cer.-br.c.</i> , cerebro-brachial connective	<i>p.p.</i> , posterior pedal lobe
<i>cr.p.</i> , posterior chromatophore lobe	<i>pc.l.</i> , precommissural lobe
<i>d.r.</i> , deep retina	<i>r.</i> , retina
	<i>sv.</i> , subvertical lobe
<i>f.l.</i> , fin lobe	<i>s.b.</i> , superior buccal ganglion
<i>fr.i.</i> , inferior frontal lobe	
<i>fr.s.</i> , superior frontal lobe	<i>t.</i> , tentacle
<i>i.b.</i> , inferior buccal ganglion	<i>t.g.</i> , ganglionated cord in the tentacle
	<i>tr.b.lat.-cr.a.</i> , lateral basal to anterior chromatophore lobe tract
<i>m.</i> , muscle	<i>tr.b.lat.-cr.p.</i> , lateral basal to posterior chromatophore lobe tract
<i>mag.d.</i> , dorsal magnocellular lobe	<i>tr.b.med.-fr.i.</i> , medial basal to inferior frontal lobe tract
<i>mag.p.</i> , posterior magnocellular lobe	<i>tr.fr.s.-v.</i> , superior frontal to vertical lobe tract
<i>mag.v.</i> , ventral magnocellular lobe	<i>tr.o.-b.ant.</i> , optic to anterior basal lobe tract
<i>mag.a.c.</i> , anterior magnocellular commissure	<i>tr.sv.-o.l.</i> , subvertical to optic lobe tract
<i>mag.p.c.</i> , posterior magnocellular commissure	
	<i>v.</i> , vertical lobe
<i>n.col.</i> , collar nerve	<i>v.d.</i> , dorsal vasomotor lobe
<i>n.o.</i> , optic nerves	<i>v.v.</i> , ventral vasomotor lobe
<i>n.pal.</i> , pallial nerve	
<i>n.po.</i> , postorbital nerve	<i>w.</i> , curtain of connective tissue that runs through the brain between the middle and posterior suboesophageal masses
<i>n.v.</i> , visceral nerve	
<i>n.f.a.</i> , anterior funnel nerve	
<i>n.r.c.</i> , posterior head retractor nerve	<i>w.b.</i> , white body

of the middle pedal commissure (figure 1, plate 20). The posterior suboesophageal mass consists of a central palliovisceral lobe with paired fin and posterior chromatophore lobes on its dorsal side (figure 3, plate 21). At the back of the palliovisceral lobe are the dorsal and ventral vasomotor lobes. Between the vasomotor lobes, and on either side of the palliovisceral lobe, is the posterior part of the magnocellular lobe, in front of which, forming the ventral magnocellular lobe, lie the giant fibres of the first order (figures 2, 3). Dorsally the magnocellular lobe continues round the oesophagus in front of the lateral basal lobes and joins the dorsal basal lobe (Young 1939).

The processes of the cells of the retina end in the outer layers of the optic lobes, forming a 'deep retina', which is thus analogous to the ganglion layer of the vertebrate retina (figure 2). From the deep retina the processes of other nerve cells go to the centre of the optic lobes and synapse with further cells, some of whose processes leave the optic lobes and go in the optic tract to the anterior and posterior basal lobes and to the superior frontal lobes (v. Lenhossék 1896; Kopsch 1899; Cajal 1917; Young 1960). The optic lobe also receives many afferent fibres from most of the supraoesophageal lobes. The peduncle lobes receive fibres from the optic lobes and send fibres to the anterior and posterior basal lobes from which they also receive afferents.

Other afferents enter the supraoesophageal lobes through the cerebro-brachial and buccal connectives. These are mainly afferent fibres from the arms (figure 4, plate 22) and the buccal mass. Afferents from the suboesophageal lobes ascend in the anterior basal and posterior basal suboesophageal connectives to the anterior and posterior basal lobes. Static nerve fibres certainly reach the medial and anterior basal lobes in this way (Thore 1939).

The medial, lateral and anterior basal lobes have no direct efferent connexions with the periphery. (In octopods a subpeduncle lobe just above the dorsal basal lobe has such efferent fibres but no homologue of this has been found in decapod cephalopods (Thore 1939; Boycott & Young 1956)). The dorsal basal lobe in *Octopus* and *Sepia* sends nerves to the optic glands. The optic glands are, however, probably a derivative of the brain (Boycott & Young 1956), so that this is not strictly a peripheral efferent pathway.

The suboesophageal efferent fibres of the medial basal lobe go to the posterior suboesophageal mass and the posterior pedal and lateral pedal lobes. Those of the anterior basal lobe go to the lateral pedal and anterior pedal lobes and a few to the posterior pedal lobe. There are numerous interconnexions between these basal lobes as well as distinct interbasal lobes. The lateral basal lobes, while closely interconnected with the medial basal and interbasal lobes, send their main efferent pathways to the suboesophageal chromatophore centres (figure 3, plate 21) (Boycott 1953).

Of the remaining supraoesophageal lobes, the inferior frontal receives afferents from the arms in the cerebro-brachial connective, and there are possibly some efferent inferior frontal-brachial fibres in this connective going to the brachial lobe. The inferior frontal lobe is also connected to the superior buccal ganglion through the cerebro-buccal connective (Hillig 1912) and there is a separate tract joining the inferior frontal lobe and the medial basal lobe (figure 1, plate 20).

The superior frontal lobe receives fibres from the optic lobes, the inferior frontal lobe and the vertical lobe. Its efferent fibres go to the vertical and subvertical lobes (figure 4, plate 22). The subvertical lobes receive fibres from the cerebro-brachial connective, from the superior frontal lobe and from the vertical lobe. The subvertical lobe is an important station on the efferent pathway of the vertical lobes (Sanders & Young 1940; Boycott & Young 1955, 1957). The majority of its fibres go to the optic lobes; some may go to the precommissural and medial basal lobes. The dorsal basal lobe is in close connexion with the olfactory, peduncle and optic lobes. Most of its efferent pathways go to these and to the optic glands; some may go to the medial basal lobes.

The gross anatomy of the peripheral nervous system has been described by Hillig (1912). More recently Martoja & May (1956), and Rossi & Graziadei (1958) have described the structure of the arms and their ganglia. Afferent and efferent fibres enter and leave the brain through the nerves of the suboesophageal lobes. Most of the nerves are mixed. Peripherally the efferent fibres of the suboesophageal lobes either end on the cells of peripheral ganglia, as in the case of the nerves to the arms, or on the effectors directly, for example, the chromatophore fibres (p. 527). Fibres from the supraoesophageal lobes descend to the suboesophageal centres mainly in the posterior basal-suboesophageal connective, the anterior basal-suboesophageal connective and the magnocellular lobe. There are only two direct connexions between the suboesophageal lobes and the optic lobes; these are to the magnocellular lobe and the lateral pedal lobes. The neuropils of the middle and posterior suboesophageal masses are continuous and tracts pass between the two. A particularly notable tract in this region is that from the posterior part of the pedal lobe to the fin lobe (p. 524). The anterior suboesophageal mass is joined to the middle suboesophageal mass by tracts from the anterior pedal lobe, although many efferent fibres go out in the brachial nerves without synapse in the anterior suboesophageal mass (brachial lobe). The anterior suboesophageal mass is, however, connected with the posterior suboesophageal mass by the brachio-palliovisceral connectives (figure 2, plate 20), which contain fibres running in both directions. This connective also contains a brachio-interbasal tract and a brachio-optic tract. The existence of the latter has received some electro-physiological confirmation recently (MacNichol and Love 1960). Fibres of the static nerves end in the lateral and posterior pedal lobes, the magnocellular lobe and the palliovisceral lobe. The lateral pedal lobe contains the cell bodies of the nerves going to the muscles of the eye and presumably receives afferents from the structures in the orbit and surrounding tissue (Boycott 1960).

The main connexions of the magnocellular lobe have been described by Young (1939) for *Loligo*. They are substantially similar for *Sepia*.

3. METHODS AND TERMINOLOGY

In all the experiments described here stimulation has been carried out using an electronic stimulator. Except where stated to the contrary, the strength of stimulus was about 1.0 V, with respect to earth, the duration of impulse about 3 ms and the frequency of stimulation about 60/s. The stimulating electrode was

varnished constantin (Eureka) wire, 32 s.w.g., which was applied to the brain by hand. This was quickly and easily manipulated and for the purposes of this work stimulation was more readily carried out in this way than through a more elaborate and non-polarizable electrode. The indifferent electrode was of sheet copper in the bottom of the dish in which the experiment was done. This was convenient because when the animal moved it did not lose contact with the electrode.

Early experiments were performed under light urethane anaesthesia; later unanaesthetized animals were used. This is essential if the maximum variety of responses from a lobe is to be obtained. Because of the violent movements made by the mantle no attempts were made to maintain the gills oxygenated with a stream of fresh sea water. Many parts of the brain could be reached without damage to the rest of the brain, for example, the vertical, medial and lateral basal lobes. With practice, stimulation of these centres could begin within 3 to 4 min of removal of the animal from the storage tank. For less accessible parts of the brain, such as the anterior basal lobe and the anterior and middle suboesophageal masses, further dissection was necessary. For access to the anterior basal lobe a horizontal cut was made at the level of the lower edge of the superior frontal lobe, thus removing all the structures above that level. The interbasal, medial basal and precommissural lobes could all be reached with that approach. The middle suboesophageal mass was stimulated after removal of all the supraoesophageal lobes. It was usually about 5 to 6 min after removal of the animal from the storage tank before stimulation of those parts of the brain was begun. The brain dies quickly under these conditions, particularly the supraoesophageal lobes, so that speed is essential. All observations were completed within 15 to 20 min of removal of an animal from the tank, and each was confirmed on not less than six different animals; the responses of several lobes were investigated in each animal. Since spontaneous responses might occur, care was taken by repeated stimulation to confirm that any given observation coincided with the application of the current to the brain.

The side of the brain on which the electrode was placed is referred to as the ipsilateral side and responses confined to that side as ipsilateral responses; to the opposite side as contralateral. The orientation of the animal used is not the morphological one (Pelseneer 1906), but that which it usually keeps when alive (Hoyle 1886). The two arms used to shoot out at the prey are called tentacles to distinguish them from the short arms that hold the prey and perform various other activities (Tompsett 1939).

4. RESULTS

(a) STIMULATION OF THE SUPRAOESOPHAGEAL LOBES

(i) General results of previous work on the supraoesophageal lobes and on the vertical lobe complex and dorsal basal lobes of cephalopods

Von Uexküll (1895) and Polimanti (1913) concluded that the supraoesophageal lobes worked through the suboesophageal lobes to produce 'movements of the body'. Sanders & Young (1940) gave a more detailed expression to this idea (p. 526). They regarded the suboesophageal centres as the final common pathways to the

periphery on which two main classes of supraoesophageal centres worked. (1) The correlation centres, those parts of the supraoesophageal lobes which were inexcitable by electrical stimulation, whose efferent pathways had at least one further synapse in another correlation centre, or in the optic lobes, before any activity in them could reach the higher or lower motor centres. (2) The higher motor centres, which included the anterior, medial and lateral basal lobes, whose main efferent pathways ended on the lower motor centres of the suboesophageal lobes. Their stimulation, in contrast to stimulation of the lower motor centres, produced complex and varied movements involving numerous effector systems.

Bert (1867) obtained no responses from any of the supraoesophageal lobes of *Sepia* during faradic stimulation and for this reason called them silent areas. He included all parts of the optic lobes in this category: this was a mistake (p. 518). He also removed all the supraoesophageal centres and described his animals as remaining immobile 'without any voluntary determination' (see p. 509). L. Fredericq (1878) reported that octopuses without the supraoesophageal lobes reacted automatically, remained completely passive and were incapable of spontaneous movements. The supraoesophageal lobes were, therefore, 'le siège du processus psychiques'. Steiner (1890, 1898) removed the supraoesophageal lobes on one side without obtaining any change in behaviour. When he removed the top part of the supraoesophageal lobes he obtained animals whose walking, swimming and visual responses were all unimpaired. But they showed no 'intelligence' or 'attention' to their surroundings and were unable to act spontaneously—they behaved like 'idiots'. It is difficult to know what structures these authors had damaged (p. 509). They could not, as they claimed, have removed all the supraoesophageal lobes, since they obtained none of the motor defects found by Buytendijk (1933) and Boycott & Young (1950), nor could they have removed only the vertical and superior frontal lobes. Their interpretations and observations seem biased by late nineteenth-century controversies concerning the 'seat of intelligence' (Schäfer 1900; Loeb 1901).

Von Uexküll (1895) was the first to show that not all of the supraoesophageal lobes were electrically inexcitable. He was unable to excite the superior frontal lobe (first cerebral ganglion) and vertical lobe (second cerebral ganglion), but obtained motor responses from the anterior and posterior basal lobes (central ganglia 2 and 3, p. 510). He removed the vertical and superior frontal lobes surgically in *Eledone* and claimed that his animals became hyperexcitable as a consequence. All their reflexes 'seemed increased' and there was an incessant play of colours all over the body. When anyone approached the tank the animals swam violently away, although normal animals in the same tank did not. From these observations von Uexküll concluded that the vertical and superior frontal lobes were inhibitory centres.

In *Octopus* Boycott & Young (1955) were unable to detect hyperexcitability after removal of these centres, either singly or together. Sanders & Young (1940) did not record hyperexcitability in *Sepia* after comparable lesions and controls. Indeed these three authors have emphasized that *Octopus* and *Sepia* appear normal after vertical and/or superior frontal lobe removal. Almost certainly the hyper-

excitability claimed by von Uexküll (1895) was due to the trauma of the operative procedures. Boycott (unpublished) has observed *Eledone* to be hyperexcitable in von Uexküll's sense after urethane anaesthesia and incision into the cranium without neural damage. Such excitability passed off after a few days. Fröhlich (1904) made a similar claim of hyperexcitability in *Eledone* after statocyst removal, and this also has been shown to be due to 'operative shock' (Boycott 1960).

Sanders & Young (1940) in *Sepia* returned to Bert's conception of electrically inexcitable areas in the supraoesophageal lobes, restricting them to the vertical, superior frontal and inferior frontal lobes. They further showed that these lobes are concerned in learning and hunting behaviour. Since then there has been abundant confirmation of the fact that the vertical and superior frontal lobes of cephalopods have an important role to play in memory (Young 1961). Thore (1942) criticized Sanders & Young's experiments on the grounds that the vertical lobe efferent fibres did not end in the subvertical lobe (which, therefore, he did not recognize). He regarded the vertical lobe complex as a part of the 'visual' system. His histological conclusions were not supported by experimental lesions to demonstrate the fibre connexions of the vertical lobe, as were those of Sanders & Young, whose main anatomical conclusions have since been confirmed by Boycott & Young (unpublished) in *Sepia* and *Octopus*.

The behavioural effects of lesions to the regions under the vertical lobe, i.e. the dorsal basal and subvertical lobes, are difficult to observe and to describe. It is now well established that octopuses and cuttlefishes without the vertical and superior frontal lobes appear in no way abnormal and completely without motor defects, those with lesions slightly deeper, thus going into the dorsal basal lobe, are also without gross motor defects, but there are, at least in *Octopus*, slight changes in behaviour that mark them off from normal animals. Thus Boycott & Young (1955) have shown that lesions in the region of the lateral superior frontal lobe interfere with the ability of an *Octopus* to attack objects placed at a distance. Lesions in the dorsal basal lobe produce octopuses that do not regularly return to their homes, change their position in a tank rather frequently and are more often than normally found seated on the side of the tank. It is probable that Buytendijk's (1933) octopuses, that could not escape from a shallow tank from which normal octopuses readily escaped, due he thought to vertical and superior frontal lobe lesions, included animals with additional lesions in these regions. Such lesions probably account also for the descriptions, such as loss of 'attention' and 'intelligence' in Bert (1867), Fredericq (1878), and Steiner (1890, 1898). A part of the dorsal basal lobe has been shown to innervate the optic gland, which controls the growth of the ovary and testis (Boycott & Young 1956; Wells & Wells 1959).

Stimulation of the vertical lobe complex and the dorsal basal lobes in Sepia

In the present experiments stimulation of the vertical, superior frontal, subvertical and dorsal basal lobes produced no behavioural responses. With a stimulus frequency of 60/s and a duration of 3 ms the voltage was varied in 0.5 V steps to about 3.5 V without any response. At 4.0 V responses due to stimulus diffusion occurred and could equally well be obtained by placing the electrode in the fluid

surrounding the brain. All the responses listed by Polimanti (1913) as being evoked from the vertical lobes were obtained in this way. With constant voltage (3·0 V) and varying the frequency from 10 to 440/s, or the duration from 0·68 to 98 ms, no responses could be obtained from these lobes. These centres, therefore, have to be regarded as silent areas.

(ii) *Stimulation of the higher motor centres—the medial, lateral, interbasal and anterior basal lobes*

Previous work on stimulation of the cephalopod basal lobes

Von Uexküll (1895) in *Eledone* and Polimanti (1913) in *Sepia* recognized three supraoesophageal centres, which they regarded as the motor centres controlling the suboesophageal lobes. Of two of them, the inferior frontal and anterior basal lobes (central ganglia 1 and 2), they have little to say. They made no anatomical distinction between the parts of the posterior basal lobe (central ganglion 3), but they identified in that lobe a centre for expiration, a centre for inspiration and a centre for swimming. In addition they obtained general chromatophore movements from all parts of the lobe. These responses are confirmed and extended here for *Sepia*, but with the important distinction that there is no evidence for distinct localizable centres of inspiration, expiration and swimming within the posterior basal lobe (p. 530). And the dorsal basal and subvertical lobes (parts of their central ganglion 3) are discovered to be silent areas (p. 529).

Present experiments on stimulation of the basal lobes in Sepia

Anterior and medial basal lobes and the control of the mantle, funnel and collar during swimming and breathing.

The main propulsive force when a cuttlefish swims, comes from jets of water pushed by the mantle musculature out of the mantle cavity and through the funnel. Similar, but gentler, movements serve for breathing. The medial basal lobe is primarily responsible for the control of the suboesophageal centres concerned with the movements of the mantle, collar and funnel during breathing and swimming. Electrical stimulation of the medial basal lobe produced gentle rhythmical inspiration and expiration of the mantle musculature and at the same time the collar and funnel worked so that water would have gone in past the collar, as during inspiration, and out through the funnel, as during expiration. The responses evoked were often rhythmical responses of this kind, not a single violent expiratory spasm, or isolated collar or funnel movements such as were obtained from palliovisceral lobe stimulation (p.). The movements induced in this way might be gentle, as if breathing, or vigorous as if swimming. Sometimes, using the same stimulus characteristics, a series of violent expiratory spasms was produced from medial basal lobe stimulation. Such a response was accompanied by folding of the fins down against the side of the body and retraction of the head and arms. This series of movements is seen when a normal cuttlefish or squid gives a giant fibre escape response (Young 1939; Boycott 1958). On such occasions ink is violently ejected from the ink sac in the normal animal and this occurred during stimulation.

Medial basal lobe control over the rhythm of the mantle musculature is not limited to breathing, swimming and giant fibre movements. Stimulation sometimes produced an inspiratory spasm so that the cuttlefish held the mantle inflated as long as the stimulus continued. Such a response may occur normally; handling a cuttlefish, the dymantic response (p. 518), irritating the funnel or collar, may all produce inspiratory spasms so that the cuttlefish holds the mantle inflated.

Anterior and medial basal lobes and the control of the fins

Previous observations on fin movement

No previous author has obtained movements of the fins of *Sepia* from stimulation of the supraoesophageal lobes, except Polimanti (1913) with suprathreshold stimulation of the vertical lobes (p. 509). In the normal animal fin movements are closely co-ordinated with the main propulsive thrust of the jets of water sent out through the funnel by the mantle musculature. Boycott (1956, 1958) has suggested that the fins are mainly concerned with giving stability to the mantle and visceral mass, aiding in steering and, perhaps, since cuttlefishes are slightly buoyant (Denton & Gilpin-Brown 1959), aiding the animal to maintain its station in the water. They, therefore, enter into several different motor activities, and correspondingly the fins are found to be under the control of both the anterior and the medial basal lobes.

Movements of the fins produced by electrical stimulation

In three experiments stimulation of the anterior basal lobes produced waves, which were always in both fins but proceeded in various directions. Sometimes they began anteriorly on the ipsilateral side and posteriorly on the contralateral side. At other times the opposite combination was observed. Both these combinations occur during normal turning (figure 7c, d). Fin waves beginning posteriorly on both sides as in swimming backwards, or anteriorly as in forward swimming (figure 7a, b) were all obtained. In all these experiments the fin waves clearly began and ended with the application of the stimulus. They were not produced as a result of struggling. The direction of the waves was independent of the position of the electrode.

Similar fin waves were obtained from stimulation of the medial basal lobe, all combinations of fin waves of which the animal is capable were obtained. Fin waves were more easily elicited from the medial basal lobe than from the anterior basal. This may be due to the fact that the former is more accessible than the latter. During the giant fibre movements elicited from the medial basal lobe the fins were shut down against the mantle (see above).

Anterior and medial basal lobes and the control of positioning of the head, eyes and arms

Previous experiments on the supraoesophageal control of cephalopod eye movements

Magnus (1902) and Krusius (1909), in *Octopus*, claimed eye movements from stimulation of what was probably the medial basal lobe, but not from the anterior

basal lobe. These observations were criticized by v. Weel & Thore (1936) who obtained eye movements only from the lateral pedal lobe (see Boycott 1960). No eye movements were obtained here by medial basal lobe stimulation.

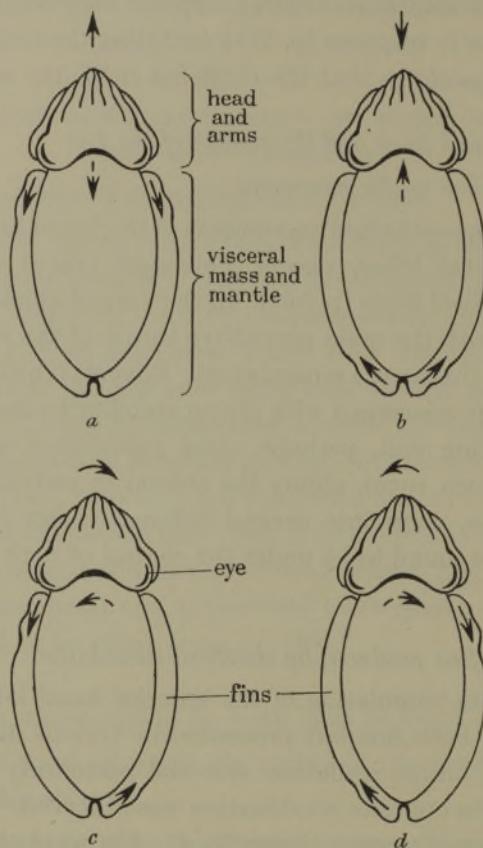


FIGURE 7. Diagrams of a cuttlefish as observed from above. The diagrams show the direction in which the animal is moving by a solid arrow; the direction of the fin waves by a solid arrow on each fin; and the direction in which the funnel is pointing by a broken arrow. Diagram *a* is of an animal going forwards, *b*, backwards, *c*, to the right, *d*, to the left.

Present results

While swimming a cuttlefish may change direction by means of its funnel and fins, the head, arms and eyes all changing their relative positions. These movements are chiefly under control of the anterior basal lobe, stimulation of any part of which may give rotation of the head and eyes. In some cases the retractor muscles of the head on the stimulated side contracted and those on the opposite side relaxed, the head being rotated towards the ipsilateral side. During these movements the contralateral eye rotated forwards and the ipsilateral eye backwards. At other times the head and eyes were rotated the opposite way.

Stimulation of the anterior basal lobe at a threshold of approximately 1.0 V might give head responses in isolation but they were usually accompanied by corresponding movements of the arms and eyes. While the head was being rotated the arms were moved either towards the side to which the head was rotating, or in

the opposite direction. Less commonly the arms were moved to one side or the other without corresponding movements of the head. In two animals movements of the eyes were observed without any other movements.

All the above movements are recognizable as part of a cuttlefish's normal behaviour, as, for example, when an animal turns to attack a prawn. Unfortunately, it was difficult to observe the funnel positions during these experiments, but in two animals, during head rotation induced by anterior basal lobe stimulation, the funnel was pointed in the opposite direction to the rotation of the head (figure 7c, d). During these experiments there was also a slight alteration in the rhythm of the mantle such as occurs during normal turning movements but there were no corresponding fin movements.

Anterior basal, medial basal and interbasal lobes and the control of seizure of food

Previous observations on cuttlefish feeding

The initial response of a cuttlefish to prey in its visual field is to raise the first pair of arms vertically upwards and sometimes partly to raise the second pair of arms. Such a sign of 'attention', as Sanders & Young (1940) have called it, has been suggested by Holmes (1940) to serve to distract the prey from its impending fate. It is possible, however, that it is part of a preparatory response preceding the ejection of the tentacles. As D. P. Wilson's (1946) photographs show, immediately before the tentacles are shot out to seize the prey all the arms are reflected back over the head. Cuttlefishes usually approach within a tentacle's length of their prey and grasp it by a sudden extension and retraction of the two tentacles together (Boycott 1958).

Seizure of food produced by electrical stimulation

Movements of the tentacles could be obtained from stimulation of the interbasal lobe (figure 6, plate 20). In the living *Sepia* the tentacles are held tightly coiled up in pockets underneath the eyes (figure 2, plate 20). It is difficult to draw them out of the pockets. If this is done forcibly it requires a considerable pull and they are withdrawn immediately they are released. In some experiments, in order to observe the tentacles adequately, an eye was removed and a hole cut in the dorsal wall of the tentacular sac. Stimulation of the interbasal region usually only produced ipsilateral responses, but sometimes bilateral ones were observed.

Three kinds of tentacle responses were seen.

(1) Sudden violent extension of the tentacles occurring at apparently irregular intervals as long as the current was applied. This corresponds to normal quick extension at the moment of seizure of the prey (Boycott 1958).

(2) Gentle extension movements, which appeared only to affect the musculature at the base of the tentacles. The result of this was that the tentacles writhed in their pockets. This corresponds to the protrusion of the tentacles between the tips of the arms just prior to being shot out at the prey (Boycott 1958).

(3) Writhing movements of the tentacles similar to those described above, but which were due to the shortening of the tentacles in the confined space of the

tentacular pocket. That it is in fact retraction and not partial extension of the tentacle has been confirmed by holding on to one, when a definite pull on the hand could be felt while the brain was being stimulated.

Prey hit by the tentacles is pulled in and held by the suckers and the arms. During stimulation of the anterior basal lobe the arms resting on the experimenter's hand were sometimes felt to make grasping movements, a response suggesting that of holding prey. Attention movements were obtained from anterior and medial basal lobe stimulation; reflexion of all the arms back over the head was obtained only from anterior basal lobe stimulation.

Inferior frontal, buccal and medial basal lobes and the control of eating

Previous experiments on cephalopods

Von Uexküll (1895) claimed two antagonistic centres in the supraoesophageal lobes of *Eledone*, one controlling the prehension and the other the release of the suckers and Polimanti (1913) using *Sepia* agreed with this. No such antagonistic systems have been found here by electrical stimulation. Von Uexküll (1895) believed that the inferior frontal lobe, buccal and brachial ganglia controlled the act of eating (Fressakt); by this he presumably meant the movements of the arms and suckers while holding and manipulating the prey. Chewing and swallowing he made specifically functions of the bucco-intestinal system. Other activities, such as swimming, ejection of ink, movements of the arms during walking, were the function of the posterior half of the supraoesophageal lobes.

Polimanti (1913) supplemented von Uexküll's observations by showing that chewing and swallowing are controlled by the 'bucco-intestinal' system, the basal lobes producing chewing by working through the buccal ganglia.

The inferior frontal lobe is a small structure in *Sepia* (figures 1, 4, 5, plates 20 to 22), but is much larger and more elaborate in *Octopus* (Wirz 1959). In *Octopus* electrical stimulation produced no responses from this lobe (Boycott & Young, unpublished). Wells & Wells (1957a, b) have shown that it is an important centre for tactile learning in *Octopus*.

Present results

In the present experiments, biting movements of the jaws have been obtained from stimulation of the superior and inferior buccal ganglia and movements of the buccal mass from stimulation of the medial basal lobe—the latter presumably mediated through the medial basal-inferior frontal tract (figures 1, 6; plates 20, 22). No such movements were obtained from the anterior basal lobe. To this extent the observations of von Uexküll (1895) and Polimanti (1913) have been confirmed.

In *Sepia* stimulation of the inferior frontal lobe between 0.5 and 1.0 V produced very slight movements of the buccal mass. At higher voltages there was diffusion to the adjacent anterior basal lobe. The mechanisms for the control of eating in *Sepia* thus probably involve the medial basal and inferior frontal lobes together with the buccal ganglia to which the latter is connected (Hillig 1912). From the buccal ganglia run sympathetic and other nerves, for example, to the salivary glands, which presumably control other phases of eating and digestion such as

salivary secretion (Hillig 1912; Pfefferkorn 1915; Bacq & Ghiretti 1953). But observations on these aspects of activity have not been made here.

Lateral and medial basal lobes and the control of chromatophore and skin movements

Previous experiments on cephalopods

Phisalix (1892, 1894) using *Sepia* decided that in the suboesophageal ganglia there was a centre or centres for excitation of the chromatophore muscles. These are now identified, p. 523. She thought the suboesophageal centres were controlled by two centres in the supraoesophageal lobes, an excitatory and an inhibitory centre. There was no detailed anatomical localization. Sereni (1930) subscribed to a similar scheme. Boycott (1953) has given a preliminary description of the chromatophore centres in several cephalopods including *Sepia*.

Present results

The lateral basal lobe is the higher motor centre controlling expansion of the chromatophores and raising of the skin papillae down one side of the body. The efferent tracts from one basal lobe go only to the anterior and posterior chromatophore lobes of the same side. They are probably the only supraoesophageal fibres which the chromatophore lobes receive (figures 3, 6; plates 21, 22). Stimulation of either of the lateral basal lobes produced uniform expansion of the chromatophores and erection of the skin papillae. Sometimes the changes were ipsilateral, and sometimes bilateral. The responses were on the head and arms as well as the mantle. No contraction of the chromatophores to produce paling was observed. Higher stimulus strengths were more likely to produce bilateral responses than weaker stimuli, but bilateral responses were sometimes obtained with threshold shocks.

Expansion of the chromatophores and erection of the skin papillae were also obtained from stimulation of any part of the medial basal lobe. The changes were sometimes ipsilateral but included the head, arms and mantle; more often they were bilateral. Unlike the responses obtained from the lateral basal lobes there were also responses in which the chromatophores contracted to produce paling of the body. These paling responses had the same distribution as the darkening responses and were sometimes ipsilateral and sometimes bilateral. Occasionally there were combinations of chromatophore expansion and contraction such that, for example, the head and arms darkened while the visceral mass paled. Other combinations of this kind, never seen in a normal animal, sometimes occurred. No undoubted signs of patterns of which the normal animal is capable were produced by electrical stimulation of the medial or lateral basal lobes (see, however, optic lobes, p. 518).

General statement of the relative roles of the individual basal lobes in the motor control of behaviour as shown by the present experiments.

From the fact that electrical stimulation of the anterior basal lobe may evoke turning of the head and eyes and a corresponding movement of the arms, it is clear that the anterior basal lobe controls the movements of these structures in such aspects

of the behaviour of the animal as orientation towards its prey. Similarly the funnel and the fins may be activated by anterior basal lobe stimulation as if to produce turning movements of the animal, movements that a normal animal makes when it is steering in and out among the rocks of its environment or on to its prey. During such movements of the normal animal there are adjustments of the rhythm of beating of the mantle and these also have been obtained by anterior basal lobe stimulation, although only infrequently. The anterior basal lobe, therefore, has control over some aspects of the posture, swimming and steering of the animal and probably of the fixation of visual objects. There is some evidence to support this from the results of unilateral lesions to the anterior basal lobe in *Sepia* (Boycott & Young 1950).

Changes in the rhythm of beating of the mantle musculature are primarily under the control of the medial basal lobe, both as far as the depth and rate of breathing are concerned and for the more powerful movements concerned with swimming. Unlike the anterior basal lobe the medial basal lobe can activate the giant fibre system of the magnocellular lobe. During such rapid escape movements the medial basal lobe exerts control over the position of the arms and head, which are retracted, and over the fins, which are shut down against the sides of the mantle. Although stimulation of the medial basal lobe evokes movements of the funnel and collar, these movements are ones associated with the breathing and swimming movements of the mantle. Medial basal lobe stimulation does not alter the direction in which the funnel is pointing, as is necessary for steering movements. It does, however, bring the funnel into the midline, as, for example, during the giant fibre response, and this is often associated with the ejection of ink, another accompaniment of the giant fibre response.

There are numerous connexions between the basal lobes, and it is impossible with the kind of experiment done here to define completely the separate and joint functions of the two lobes. They must inevitably function together to produce complex patterns of behaviour, presumably the one dominating over the other according to the varying sensory inputs. This is well illustrated by the tentacles. The cuttlefish only protrudes its tentacles as the end-point of a complicated behaviour sequence involving the eyes, fins, mantle and the positioning of the head and arms. The anterior and medial basal lobes control those movements, yet tentacle movements are never obtained as a result of their stimulation. The interbasal lobe, which lies between these lobes, is the tissue responsible for initiating the final act by which prey is seized, although the anterior basal lobe controls the holding of the prey; and the medial, inferior frontal and buccal lobes the act of eating. It is possible that a great deal of the integration of these lobes occurs through their complicated afferent and efferent connexions with the centre of the optic lobes.

(iii) *Summary of the present results of stimulation of the supraoesophageal centres
Silent areas*

No movements were seen after stimulation of the vertical, superior frontal, subvertical and dorsal basal lobes, or the precommissural lobe.

Anterior basal lobe

Protraction, retraction and rotation of the head; eye movements; movements of the arms, including reflexion of all of them over the head, raising of the first, or the first and second pair of arms to the attention position, placing of the arms together in the midline, grasping movements; slight changes in the respiratory rhythm of the mantle; fin waves; funnel movements; no chromatic changes.

Lateral basal lobe

Expansion of the chromatophores of all parts of the body; movements of the skin, including erection of the skin papillae.

Medial basal lobe

Protraction and retraction of the head, but no head rotation; placing the arms together in the midline; raising of the first and/or second pair of arms to the attention position; respiratory and swimming movements; giant fibre responses; fin waves; movements of the buccal mass; expansion and contraction of the chromatophores, sometimes giving crude patterned responses.

Interbasal lobe

Movements of the tentacles including extension and retraction.

Superior and inferior buccal ganglia; inferior frontal lobe

Movements of the buccal mass and tongue.

(b) STIMULATION OF THE OPTIC COMPLEX

(i) *Previous work on stimulation of the optic lobes of cephalopods*

Bert (1867) obtained no response to electrical stimulation of the optic lobes and therefore called them silent areas. Von Uexküll (1895) in *Eledone* obtained ipsilateral or bilateral changes in the colour of the skin, erection of the skin papillae, darkening of the mantle eyespots, breathing and swimming. Polimanti (1913) obtained substantially similar responses in *Sepia*. He claimed also to have identified three separate parts to each optic lobe: (1) An anterior part which, when stimulated, produced rotation of the eyes upwards and backwards, inspiratory spasms and unilateral chromatophore movements. (2) A middle part giving much the same responses but more extensive chromatophore movements. (3) A posterior part which, when stimulated, evoked movements of the eyes upwards and forwards and produced expiratory spasms. No evidence for such localization was found here. Sanders & Young (1940) found that the outer parts of the optic lobes are electrically inexcitable and electrical stimulation of the central part of the optic lobes evoked responses from many of the effector systems of the body. It is shown here that only to this extent is there localization within the optic lobes.

Recently MacNichol & Love (1960) have recorded 'on' discharges from the optic nerves of squid but not 'off' discharges. With an electrode thrust into the optic lobes they found 'on' and 'off' discharges and 'spontaneous' activity and tactile responses (see p. 506).

(ii) *Optic nerve stimulation*

Cutting the optic nerves appeared to produce expansion of the chromatophores of the whole animal and sometimes expiratory movements and turning of the arms towards the side on which the cut was made. These responses were due to the incidental cutting of the connective tissue carrying sensory fibres from the eye muscles and the skin surrounding the eye. When the optic nerves alone were cut, or when they were stimulated electrically, no responses occurred.

(iii) *Optic lobe stimulation*

Three types of colour change have been obtained from the optic lobes, expansion of the chromatophores (darkening), relaxation of the chromatophores (paling), and a differential expansion and relaxation of the chromatophores (patterning). General expansion of the chromatophores is obtained at lower thresholds than the other responses and may be unilateral or bilateral. Very occasionally contralateral responses occurred without a corresponding change on the ipsilateral side. Using strengths of stimuli which only just produce darkening a colour change is as likely to be bilateral as with stronger stimuli. The expansion of the chromatophores included those on the head, arms and mantle.

The patterned response most frequently obtained was that of the white square and white band on a chocolate-coloured background. The light mottle pattern and the zebra pattern were also obtained. [The generally used categories of chromatic response are described by Holmes (1940).] Occasionally the black spot was elicited ipsilaterally or bilaterally without any other colour change. The patterns were often, but not always, bilateral. Relaxation of the chromatophores to produce uniform paling was obtained more often than patterning, but less often than darkening. A type of patterning not observed in the normal animal was obtained when the mantle and fins darkened bilaterally and the head and arms paled bilaterally, and vice versa. Erection of skin papillae often accompanied the colour changes, except those involving paling.

Fin waves were obtained several times from stimulation of the optic lobes and included all possible combinations of directions and positions of the funnel (figure 7). The fins were sometimes brought up dorsally and flattened against the back which has never been observed in normal behaviour. The reverse movements, flattening of the fins against the underside of the body, were obtained more frequently and were usually accompanied by giant fibre contractions of the mantle.

Protraction or retraction of the head were often seen, the latter often accompanied by giant fibre movements of the mantle. Rotation of the head towards the stimulated side sometimes occurred. There was also flattening of the head and body against the bottom, together with rotation of the eyes upwards. This is a dymantic* response, given in a normal animal in response, for example, to a predator. It presumably evokes avoidance responses in the predator.

* Dymantic is a term coined by Young (1950) to categorize patterns of colour and behaviour which presumably serve to startle a predator and so ward off an attack (see also Boycott 1958).

A variety of well-defined arm movements were evoked. Raising of the first pair of arms into the attentive position was rather frequent and this might be accompanied by raising of the second pair of arms. Flexion of the arms and their spreading back over the head (p. 513) was also seen. The tentacle movements described on p. 513 were obtained from optic lobe stimulation and grouping of the arms together in the midline.

Movement of the arms to one side or the other was also obtained, and this movement was sometimes sufficiently great to produce the touched back response (p. 522). In one male stimulation produced lateral extension of the ipsilateral fifth arm. (This movement is performed in the normal animal when a male approaches a female, in which case it may be succeeded by copulation. If the approached animal is another male, that animal will extend its fifth arm and the approaching male will swim away (Bott 1938; Tinbergen 1939).

The optic lobes also have control over the activities of the mantle musculature and funnel. Their stimulation produced changes in the rate of breathing of the mantle. There were exaggerated inspiratory spasms such as are seen in the normal animal when it is picked up in a net.

Stimulation of the optic lobes sometimes produced ejection of ink, particularly when a giant fibre movement was evoked.

(iv) *Peduncle and olfactory lobes, previous work and present results*

No new results have been obtained in these experiments. Klemensiewicz (1878), von Uexküll (1895) and Polimanti (1913) concluded that the peduncle lobe was a chromatophore centre. They did not recognize an olfactory lobe. The peduncle and olfactory lobes are so close together that it is impossible without special methods to stimulate them separately (Boycott & Young 1956).

In the present experiments when an electrode was placed on them at a threshold of 1.0 to 1.5 V expansion of chromatophores all over the body occurred. This confirms results of previous workers. With very slightly stronger stimulation a wide variety of responses, such as occurred after stimulation of the optic lobes, was seen. The peduncle and olfactory lobes lie so close to the optic tract that it was impossible to be sure that the responses were not due to diffusion of the current to adjacent optic tract fibres.

However in *Octopus* (unpublished) it has been possible to isolate the peduncle and olfactory lobes on the optic tract by removing the optic lobes and waiting until the optic tract fibres had degenerated. Stimulation of the peduncle and olfactory lobes in such preparations showed that they can elicit a wide variety of activities. Experiments of this kind could not be done in *Sepia*, but it is probable, in view of the similarity of its connexions with those of *Octopus*, that the range of function of the peduncle lobe in *Sepia* extends beyond chromatic control.

(v) *Optic tract stimulation*

By stimulation of the optic tract all the responses which could be obtained from stimulation of the centre of the optic lobes were seen.

(vi) *Summary of the present results of stimulation of the optic complex**Optic nerves*

No responses.

Optic lobes

The periphery of the optic lobes is electrically inexcitable.

Stimulation of the centre of the optic lobes evoked all the responses which it is possible to get from the medial, lateral, interbasal and anterior basal lobes. In addition there were some responses not obtained from, but presumably mediated by, these lobes. They included some patterns of chromatic activity, drawing of the arms together in the midline and lateral extension of the fifth arm in a male. No eye movements were observed but have been claimed by Polimanti (1913).

Peduncle and olfactory lobes

Chromatophore expansion.

Stimulation of the *optic tract* has confirmed all these responses.

(c) STIMULATION OF THE SUBOESOPHAGEAL LOBES

(i) *Anterior suboesophageal mass*

In the present experiments the brachial lobe has been stimulated only after removal of all the supraoesophageal lobes. Application of the cathode to any part of the dorsal side of the lobe at a stimulus strength of 0.5 V produced no responses; but at 0.7 V movements of all the arms on both sides of the body were obtained. The movements were unlike any normal movements made by a cuttlefish. They appeared, in fact, to be a simultaneous unco-ordinated contraction of circular, longitudinal and oblique muscles, resulting in the arms being extended and held rigid.

These observations contradict those of Sanders & Young (1940) who obtained movements of the kind described above but of one arm at a time at threshold strengths. The explanation of the difference is anatomical. Many of the efferent fibres that go to make up a brachial nerve do not originate in the brachial lobe, but come from the anterior pedal lobe. These pedal fibres form well-defined tracts, which pass through or under the brachial lobe on their way to the brachial nerves. It is probable that Sanders & Young (1940) were stimulating these roots and so getting isolated responses of individual arms. By a similar error Polimanti (1913) separated the brachial lobes into a dorsal 'chromatophore part' and a ventral 'arm movement part'. In the present experiments if the stimulating electrode was thrust into the brachial lobe, near the pedal roots of the brachial nerves, movements of individual arms were obtained. An arm activated in this way extended outwards from the mouth and was held rigid as long as the stimulus was maintained. The chromatophores of the arm also expanded. Such a movement, together with expansion of the chromatophores, was identical to that obtained when a brachial nerve was dissected out within an arm and stimulated directly.

Stimulation of the brachial lobe proper, that is by application of the electrode to the dorsal surface, where the pedal efferent tracts do not run, did not produce local movements of the arms. The responses at threshold stimulation were either movements of all of the arms or none, and the chromatophores were never expanded. The tentacles were never excited by brachial lobe stimulation unless the electrode was pushed towards the underside of the lobe, which is where the pedal tracts going to the tentacular nerves lie. Innervation of the tentacles is, therefore, exclusively from the middle suboesophageal mass, as is that of the chromatophore musculature of the head and arms (p. 522).

(ii) Middle suboesophageal mass

Previous experiments on cephalopods

Bert (1867) did not separate the pedal lobe from the other suboesophageal lobes (p. 522). Polimanti (1913) found arm and chromatophore movements, ejection of ink (see p. 523), backward movements of the funnel, inspiratory movements and eye movements, although he did not localize these to any particular part of the middle suboesophageal mass. Except for the inspiratory movements these observations are confirmed and localized.

Anterior pedal and posterior pedal lobes

The anterior pedal lobe gave movements of the arms and tentacles on stimulation, the posterior pedal lobe retraction of the head and movements of the funnel, but not of the collar and mantle musculature. Protraction of the head has been obtained from stimulation of the supraoesophageal centres but not from stimulation of any suboesophageal centre. There are no muscles which could antagonize the retractor muscle system, presumably therefore head protraction is executed by controlled relaxation of the retractor muscles. Fin movements obtained from the posterior pedal lobe are described on p. 524.

Stimulation of the dorsal side of the anterior pedal lobe gave movements of the arms similar to those obtained from stimulation of the brachial lobe. When the electrode was pushed into the lobe extension of the tentacles occurred on application of the current. It was never possible, however critically the threshold was adjusted, to obtain movements of a single arm as claimed by Sanders & Young (1940). The nearest to individual movements were extension of the tentacles and raising of the first pair of arms to 'attention' (p. 513).

Some of the arm responses obtainable from the anterior pedal lobe were recognizable as definite components of normal behaviour. From the front, approximately in between the anterior chromatophore lobes, the response to electrical stimulation was generally raising of the first pair of arms as in attention; occasionally they were accompanied by erection of the second pair of arms. Such responses were obtained as far back as the beginning of the posterior pedal lobe. In that region, however, other movements, generally extension of the arms, were more common. Sometimes there was extension of the arms on one side and retraction on the other, so that the arms turned towards the ipsilateral side. This movement was very like that seen in a normal cuttlefish. When the back of a

normal cuttlefish is irritated the animal may reach round with its arms and grasp at the irritation. Young (unpublished) has shown that *Sepia* with only the suboesophageal lobes intact can show this response.

Lateral pedal lobes

The lateral pedal lobes contain the cell bodies of nerve fibres innervating the intrinsic and extrinsic muscles of the eyes. Stimulation of either produced movements of the ipsilateral or of both eyes.

v. Weel & Thore (1936) showed this in *Octopus* and in addition described pupillary dilatation.

Anterior chromatophore lobes

Stimulation of either side of the front end of the anterior pedal lobe produced expansion of the chromatophores of the front part of the head and on the arms. These regions are, therefore, named anterior chromatophore lobes. The threshold of response was somewhat lower than for other suboesophageal centres, 0.3 to 0.5 V as compared with 0.7 to 1.0 V. At 0.3 V the responses were ipsilateral only; at 0.5 V bilateral. No combinations of expansion and contraction of the chromatophores to provide patterns of colour were obtained. Nor were there any changes in the degree of expansion of the mantle chromatophores. The chromatophores of the front part of the head and arms are, therefore, innervated from these lobes. Stimulation of the anterior chromatophore lobes also gave movements of the skin and erection of the papillae of the head and arms.

Contraction of the chromatophores to produce pallor was never obtained from direct stimulation of the anterior chromatophore lobes. But such a response could often be obtained along the dorsal side of the anterior pedal lobe back to about the beginning of the posterior pedal lobe. In this case the responses were usually on the head, arms and mantle together. Sometimes there were changes on the head and arms without changes on the mantle, and vice versa.

(iii) *Posterior suboesophageal mass*

Previous experiments on cephalopods

Bert (1867) showed that stimulation of the cardiac nerves produced diastolic arrest, and he also obtained vasomotor effects from stimulation of the palliovisceral ganglion. More recent observations on the neural control of heartbeat have been made by de Wilde (1956) on *Octopus*; a general summary is given by H. Fredericq (1947). Mislin (1950) has confirmed this in *Octopus* and shown that this centre coordinates not only vessels of the visceral mass but also those of the arms (see p. 506). None of these vasomotor effects was examined here, but vasomotor lobes anatomically similar to those in *Octopus* can be recognized (figure 1, plate 20). The vasomotor fibres going to the arms run in the brachio-palliovisceral connectives and it is probably these that Mislin (1950) was stimulating when he located a vasomotor centre in the pedal lobes.

Bert (1867) also showed that the posterior suboesophageal mass controlled the respiratory movements of the mantle, collar and funnel as well as fin and arm

movements. Polimanti (1913) confirmed these results adding ejection of ink, movements of the funnel, turning the eyes forward and chromatophore movements as part of the repertoire. These results are confirmed here except for the eye and arm movements, which were not obtained.

Mislin (1955) has described spontaneous rhythmic potentials from the posterior suboesophageal mass. Mislin, Riesterer & Schroeder (1954) have recorded 'spontaneous' potentials from the posterior chromatophore lobes.

Palliovisceral lobe

In the middle of the dorsal side of the palliovisceral lobe are the cell bodies of the fibres of one of the roots of the pallial nerve. Stimulation in this region produced a violent expiratory spasm, which continued as long as the stimulus was applied (a period of about 30 s). Just posterior to this are the cell bodies of the posterior head retractor nerves, and stimulation here produced retraction of the head. Collar movements could also be evoked in this region. The posterior funnel nerve leaves the ventral side of the palliovisceral lobe and stimulation here gave funnel movements. No special region could be found where all these responses were co-ordinated so that mantle, funnel and collar worked together, as they do in the normal animal and as can be found in medial basal lobe stimulation. Stimulation of the neuropil of the palliovisceral lobe produced any or all of these movements, presumably depending on whether or not the electrode happened to be nearer one tract or group of cells than another. At threshold the responses always occurred one at a time. At higher strengths they all occurred together, but not in a co-ordinated manner. The movements of the mantle musculature on palliovisceral lobe stimulation were always expiratory.

Ejection of ink was obtained from palliovisceral lobe stimulation. Polimanti's (1913) observation of ink ejection from stimulation of the pedal lobes was not confirmed. The procedure of handling and dissecting the animal involves the ejection of so much ink that its ejection as a consequence of electrical stimulation is not easy to observe. This may explain why Polimanti thought he obtained ink ejection from pedal lobe stimulation.

Posterior chromatophore lobes

On the dorsal side of the palliovisceral lobe are four lobes, two on either side. Because it has been found here that the anterior pair produced movements of the fins on stimulation and the posterior pair chromatophore expansion, the terminology of Thore (1939), who first identified and named them as a single lobe, the *I. accessorius*, is rejected for the terms fin lobe and posterior chromatophore lobe.

The posterior chromatophore and fin lobes are invested closely by the cartilage of the cranium. This can be sliced away without damage to them or the rest of the brain. Although closely apposed they are easily recognized externally by a distinct fissure. The posterior chromatophore lobes innervate the chromatophores of the mantle, fins and visceral mass (p. 527). Their stimulation produced expansion of the chromatophores of the ipsilateral side at threshold strength. At slightly higher voltages, up to 0.5 V, bilateral responses occurred, presumably mediated by the

posterior chromatophore lobe commissure. This commissure was occasionally stimulated directly when the electrode was applied to the posterior part of the palliovisceral lobe and produced bilateral chromatophore expansion. Like the anterior chromatophore lobes stimulation of the posterior chromatophore lobes may produce erection of skin papillae.

The processes of the cells of the posterior chromatophore lobe innervate the chromatophore muscles directly. They therefore provide an opportunity for analysis without the added complexity of peripheral ganglia such as are found on the arm nerves (p. 528). The threshold of excitation of the posterior chromatophore lobes, like that of the anterior chromatophore lobes, is very low and any excitation, other than by gentle prodding of the lobe with the electrode, produces a total response of all the chromatophores of at least the ipsilateral side. However, by prodding the lobe with the electrode (i.e. mechanical stimulation) groups of chromatophores on the back could be expanded independently of the others. Prodding the anterior part of the lobe produced ipsilateral expansion of chromatophores at the front end of the mantle; prodding the middle of the lobe, ipsilateral expansion of chromatophores in the middle of the mantle; and when the chromatophore lobe was prodded posteriorly, expansion of the chromatophores at the hind end of the mantle. Expansion of the chromatophores of the mantle and fins was obtained from no other suboesophageal centres but these lobes; electrical stimulation did not, however, evoke paling or patterns of response from them.

Fin lobes and the posterior pedal-fin lobe tracts

Ten Cate (1929b) showed that the fin is innervated directly from the central nervous system and that the waves of activity are generated in the central nervous system and not in a peripheral system of ganglia and fibres. The only responses obtained from the fin lobes were movements of the fins. The movements obtained from stimulation of a fin lobe were always a raising of the ipsilateral fin, folding over of the outer edge and crimping of this edge into numerous folds. The fin was held in this position as long as the stimulus was applied. The movement was always a movement of the whole fin in marked contrast to wave movements elicited by stimulation of higher centres. The threshold of the response was between 0.3 and 0.5 V. The lobe was so sensitive that merely placing the electrode on the surface of the lobe was sufficient to start the fins twitching slightly. However, unlike the chromatophore responses under similar conditions, all parts of the fin appeared to move. Whatever the strength of the electrical stimulus the movements were always of the whole, never of parts, of the fin. With variations in frequency of stimulation from 20 to 210/s there was little difference in the responses. At higher frequencies the responses were perhaps stronger in the sense that the fin was folded and crimped more tightly.

Anatomically there is no obvious commissure between the fin lobes. This is confirmed by the fact that even with stimuli as strong as 2 V, which is nearly sufficient to cause diffusion to the palliovisceral lobe, it is impossible to get movements of the fins of both sides. The two fins commonly work together in the normal animal. Integration of their responses must therefore be in the posterior pedal

lobes and/or the supraoesophageal lobes. There are no tracts running directly from the supraoesophageal lobes to the fin lobes, but each fin lobe receives a tract the cell bodies of which lie in the walls of the posterior pedal lobe. Stimulation of the posterior pedal lobe in the region of this posterior pedal-fin lobe tract produced movements of the whole fin essentially similar to those following stimulation of the fin lobe. Sometimes a whole fin was flapped up and down in a manner never seen in the intact animal; such a response was occasionally seen during medial basal lobe stimulation.

Brachio-palliovisceral connective

This connective is difficult of access and despite its numerous connexions few responses have been evoked by its stimulation. Stimulation was carried out where the connective could just be seen at the junction of the anterior and middle suboesophageal masses. Retraction of the head, increase in rate of beating of the collar and short, sharp expiratory movements were all obtained in different experiments. These responses were obtained one at a time, never co-ordinated together. The expiratory movements were very like giant fibre responses. Presumably, therefore, the fibres stimulated were the ones going to the ventral magnocellular lobe (Young 1939).

Magnocellular lobe

The ventral part of the magnocellular lobe, which contains the first order giant fibres, has twice been stimulated successfully in these experiments, with the result that very strong expiratory spasms were obtained. No results were obtained from stimulation of the parts of the magnocellular lobe in the posterior suboesophageal mass or from the dorsal part around the oesophagus.

Von Uexküll (1891, 1895) in *Eledone* and Polimanti (1913) in *Sepia* claimed to have shown in the posterior suboesophageal mass a centre for inspiration and a centre for expiration. Von Uexküll (1895) showed that *Eledone* still has a respiratory rhythm after removal of all the supraoesophageal lobes. This has been confirmed in *Octopus* and *Sepia* (Boycott & Young 1950). Boycott (unpublished) has shown in *Octopus* that inspiration can be obtained from stimulation of the posterior magnocellular lobe and expiration from stimulation of the palliovisceral lobe, and it is probable that these two generate the basic respiratory rhythm. Support for this comes from Gray's (1960) records of electrical activity in the mantle connective of *Octopus*. Anatomically there is no reason why the magnocellular and palliovisceral lobes should not work this way in *Sepia*. Polimanti's (1913) claim that there are separate inspiratory and expiratory centres in the cuttlefish would tend to support this view, although his results were not confirmed in these experiments.

(iv) *Summary of the present results of suboesophageal lobe stimulation*

Anterior suboesophageal mass

Movements of all the arms at threshold strength. No responses from any part of the body other than the arms.

Middle suboesophageal mass

Four categories of response corresponding to anatomically definable regions are recognized.

Anterior pedal lobe

Movements of all the arms; raising of the first and sometimes the second pair of arms to the position of attention; extension of the tentacles; contraction of the chromatophores.

Posterior pedal lobe

Head retraction; funnel movements; fin movements; contraction of the chromatophores. Tentacle but no arm movements.

Lateral pedal lobe

Movements of the eyes on the side stimulated.

Anterior chromatophore lobes

Expansion of the chromatophores of the head and arms; movements of the skin.

Posterior suboesophageal mass

Four categories of response corresponding to anatomically definable regions.

Palliovisceral lobe

Contraction of the mantle musculature; movements of the collar; movements of the funnel; no responses from the arms, fins or eyes; ejection of ink.

Fin lobes

Ipsilateral fin movements.

Posterior chromatophore lobes

Ipsilateral and bilateral expansion of the chromatophores of the fins and mantle.

Brachio-palliovisceral connectives

Retraction of the head; expiratory movements; increase in rate of beating of the collar.

Magnocellular lobe

Giant fibre responses from the ventral magnocellular lobe.

5. DISCUSSION

(a) *Physiological classification of the brain of the cuttlefish*

A physiological classification of the brain of cuttlefishes was proposed by Sanders & Young (1940) based on the results of faradic stimulation. They divided the parts of the brain into four groups: (1) *Lower motor centres*, consisting of cells whose fibres either innervate the effectors, or have only one further synapse in the

periphery. Faradic stimulation of these produced movements of the parts they innervate. The movements were local. (2) *Higher motor centres*, consisting of cell bodies whose processes run to the lower motor centres and affect the periphery only through these. Faradic stimulation of these produced movements of large groups of muscles. (3) *Primary sensory centres*, including such regions as the optic lobes. Faradic stimulation of these produced movements of large groups of muscles and their responses were not always clearly marked off from those of the higher motor centres. (4) *Correlation centres*, these included the vertical, superior frontal and subvertical lobes, which were unresponsive to electrical stimulation.

(b) *Characteristics of the suboesophageal motor centres*

Sanders & Young (1940) considered all the suboesophageal lobes to be lower motor centres. It is clear from the present experiments that this is not true on the basis of their criteria.

The responses of the suboesophageal centres were local in the sense that from any one region a limited set of structures, the cell bodies of whose nerve fibres lay in the region stimulated, responded to the stimulus.

However, there is a limit to the localization of the responses that can be obtained from the lobes. The brachial lobe produced only movements of the arms, but by stimulation of the lobe alone it was impossible to get movements of a single arm. A portion of the mantle could not be made to contract by central neural stimulation, though it could by stimulation of a stellar nerve. On the other hand movement of isolated groups of chromatophores could be obtained by appropriate stimulation of the posterior chromatophore lobes. In this respect the chromatophore lobes are within Sanders & Young's definition of lower motor centres and the brachial and anterior pedal lobes, for example, are not.

(c) *Characteristics of intermediate motor centres*

The difference in response to electrical stimulation between such lobes as the chromatophore lobes and the brachial lobes is interpreted here as due to the fact that only some of the suboesophageal centres contain the final common pathways (Sherrington 1947) to the periphery. For this reason the suboesophageal lobes are considered to contain both intermediate and lower motor centres.

Hughlings Jackson (1932) recognized highest, middle (or intermediate) and lowest centres. The terms higher and lower motor centre have common currency today. While reintroducing the term intermediate motor centre no special analogy with those parts of the vertebrate brain included in Hughlings Jackson's terminology is intended.

Sereni & Young (1932) showed in *Octopus* that the fibres innervating the chromatophores did not synapse in the stellate ganglion. These fibres come from the posterior chromatophore lobe and this is, therefore, a lower motor centre. Movements of isolated groups of chromatophores can be obtained from it. The brachial lobe and the anterior pedal lobe are intermediate motor centres in that movement of a single arm or tentacle cannot be elicited by their electrical stimulation. These lobes do not innervate the muscles of the arms and tentacles directly. In each arm

and tentacle there are ganglionated cords in which some, probably all, of the fibres of the brachial and tentacular nerves synapse (with the exception, of course, of the chromatophore fibres). These ganglia are the final common pathways to the arm and tentacular muscles and have their own local reflex pathways (von Uexküll 1894; Ten Cate 1928).

The palliovisceral lobe is an intermediate motor centre in the sense that the fibres going to the muscles of the mantle all end in the stellate ganglion where there are local reflexes (Ten Cate 1929*a*; Gray 1960; D. M. Wilson 1960), but the fibres going to the funnel and collar and blood vessels innervate the muscles directly; in this respect it is a lower motor centre.* Unfortunately, details of the innervation of the muscles from the rest of the suboesophageal centres are not known. For the present, where there is a peripheral ganglion on a nerve from the suboesophageal lobes, then the region from which the nerve arises is an intermediate motor centre, for example, that part of the visceral nerve that ends in the branchial ganglion.

Ten Cate (1929*b*) showed that the fin nerve does not have any ganglia along its course. The fibres to the fin musculature have been shown here (p. 524) to originate in the fin lobe which is, therefore, to be classified on anatomical grounds as a lower motor centre. The fin lobe does not, however, behave in response to electrical stimulation as a lower motor centre. It was not found possible to produce responses from segments of the fin. This may have been due to some peculiarity of the neuropil such that if stimulated, other than by the ordered firing of the fibres from the higher motor centres and the posterior pedal fin-lobe tract, it was bound to respond as a whole; or it may have been that once an individual segment of the musculature of the fin had been made to contract there was a reflex excitation such that the whole of the fin lobe was excited.

Boycott (1960) has discussed the possible role of the lateral pedal lobes and the static nerve fibres in the control of equibrail responses and compensatory eye movements. Both these and the magnocellular lobe are to be classified as intermediate motor centres.

The category intermediate motor centre may not, of course, be as distinct from the lower motor centre category as the above discussion has implied. It may be that the movement of all the arms produced upon brachial or anterior pedal lobe stimulation was due to some mechanism of the kind suggested to explain the fin lobe responses. The category intermediate motor centre is, at present, a useful one, since it points the contrasts between the responses of the lobes and their anatomy.

(d) Characteristics of the higher motor centres

As Sanders & Young (1940) pointed out, stimulation of the higher motor centres gives movements of large groups of muscles, but such a definition does not categorize them sharply from the intermediate motor centres as defined above. The contrast is better pointed by saying that they produce combined movements of different groups of effectors, and that these movements can be obtained from stimulation of any part of a higher motor centre. Any region in the anterior basal lobe, for example, is likely to produce at the same time movements of the head,

* See addendum p. 534.

eyes, funnel and fins (see p. 530). Moreover, the responses obtained from the higher motor centres are more nearly like those shown by a normal animal. For example, the medial basal lobe when stimulated may produce rhythmical swimming movements of the mantle musculature co-ordinated with waves of activity from the fins, but stimulation of the posterior suboesophageal mass will produce expiration not rhythmical movements, and fin waves cannot be produced from the fin lobe.

The colour responses of the medial and lateral basal lobes are the exception to this generalization that the responses of the higher motor centres to electrical stimulation are more normal. Nevertheless, they are clearly higher motor centres in the sense defined above, because they control the chromatophores of all parts of the body, and paling responses as well as darkening responses can be obtained from them.

The responses from a higher motor centre may sometimes be elaborate in the sense that, for example, application of the cathode to one part of the anterior basal lobe may produce pointing of the funnel to one side accompanied by the appropriate fin waves and corresponding movements of the head, arms and eyes, as if the animal were turning. However, this is not necessarily so and any of these movements may occur individually. Such individual movements, however, are usually well co-ordinated and very like those produced by the normal animal.

(e) *Characteristics of silent areas*

Sanders & Young (1940) categorized those areas of the brain that gave no responses to electrical stimulation as correlation centres. In view of the probably varied activities of the electrically inexcitable masses of neural tissue it is perhaps best to drop the terms correlation and association centre with their connotation of learning and memory, and use the more descriptive term 'silent' area as used by Bert (1867). Sanders & Young identified in this category the vertical, subvertical and superior frontal lobes. Anatomically these centres are not connected directly with any single receptor or with the lower motor centres. On the basis of their connexions, the existence of an anatomical basis for a system of self-re-exciting chains (Young 1938) and the fact that they are electrically inexcitable, Sanders & Young (1940) predicted and proved that these centres are concerned with learning and other complex forms of behaviour, such as hunting. The present experiments have shown that the dorsal basal and precommissural lobes are also electrically inexcitable.

(f) *Characteristics of the primary sensory centres*

Primary sensory centres, such as the optic lobes, are characterized by responding to electrical stimulation in part as higher motor centres and in part as silent areas. The periphery of the optic lobes does not respond to electrical stimulation. This region is part of the mechanism of coding of retinal events into neural terms, which can then evoke a wide range of responses through the cells at the centre of the lobe (Young 1960). The fact that in all parts of each optic lobe there seem to be cells or groups of cells capable of producing equivalent patterns of behaviour is one of the most interesting results of the investigation.

Cuttlefishes depend very much in their normal environment on their ability to respond to complex visual stimuli. From the time of hatching they use their eyes

and adapt rapidly to changing conditions of visual information (Wells 1958). It is not, therefore, surprising that stimulation of the optic lobes evokes such a wide variety of responses, since events in the optic lobes are of prime importance in the animals' behaviour. It is difficult to imagine how particular visual inputs are enabled to produce specific patterns of response, whether instinctive or learned.

Unfortunately, too little is known of the responses of the peduncle and olfactory lobes to discuss the position of these as primary sensory centres or otherwise. The inferior frontal lobe is probably a primary sensory centre.

(g) Electrical excitability and inexcitability

It is generally assumed that electrical stimulation of masses of neural tissue is a very crude method of evoking the responses of which they are presumably capable. Yet it is remarkable how nearly normal the responses are that can sometimes be obtained, for example from the higher motor centres.

The fact that fin waves can be evoked by stimulation of the optic lobes, optic tract and higher motor centres, but not from stimulation of the intermediate and lower motor fin centres is a particularly clear example of the differences between the various levels of the brain in their response to electrical stimulation. It seems that the farther away from the periphery stimulation is carried out the more likely integrated responses are to occur. This is also generally true for the vertebrate brain. The fins are raised by one group of muscles and lowered by an antagonistic group. Presumably from the fin lobe there are nerve fibres going to each of these muscle groups. Electrical excitation of this lobe excites either directly or reflexly (p. 528) both groups of nerve fibres, hence the unco-ordinated response. Electrical stimulation at this level cannot imitate the presumably ordered excitation of the fibres. Nor can it imitate the ordered excitation when stimulation is one stage back from the periphery into the central nervous system (the posterior pedal-fin lobe tract). There is, however, some property a further stage back in the central nervous system, such that when higher motor centres are excited a stimulus that provides general excitation in the more peripheral centres produces more specific patterns of excitation in the higher motor centres. These experiments provide no information as to the nature of this phenomenon.

The 'silent areas' are exceptions to the generalization that more normal responses are elicited upon electrical excitation the farther the lobes stimulated are from the periphery. Since many of them control learned or other complex responses the activity aroused by stimulation cannot be recorded, as Penfield (1959) has shown it can be after stimulation of analogous areas in patients who can describe the results.

(h) Localization of responses

So far it has been assumed that stimulation of a particular lobe evokes some, if not all, of the activities for which that lobe is responsible in the course of normal behaviour. From experiments in which the optic tract was stimulated it is clear that stimulation of afferent pathways to the higher motor centres may evoke any of the responses of which that higher centre is capable. It might be, therefore, that what are described as the responses of the higher motor centres to electrical

stimulation are in fact the responses of optic afferents stimulated within the higher motor centres. However, there is some evidence that this is not so. Application of current to the cell wall at the back of the medial basal lobe produced responses exactly like those evoked when the electrode was applied to its neuropil. It might be, of course, that the current was stimulating the afferent fibres by diffusion. If this were so it would be expected that the threshold of excitation would be higher than when the neuropil was directly stimulated. It was not. In *Octopus* a few experiments have been done (Boycott, unpublished) in which the optic tracts have been cut and the optic fibres to the higher motor centres in consequence degenerated. Stimulation of the higher motor centres in such experiments produced behaviour similar to that of animals without the optic tracts cut and at a similar threshold of excitation.

Von Uexküll (1895) and others regarded swimming, breathing and other aspects of behaviour as localizable to definite centres. This is true for intermediate and lower motor centres. It is not true for the higher motor centres. In the sense that head turning movements, for example, are evoked from the anterior basal lobe and not from the medial basal lobe, while rhythmical breathing movements are obtained from the medial basal lobe and not from the anterior basal lobe, there are 'centres' within the supraoesophageal lobes. However, no evidence has been found here for localization *within* a lobe of the responses of which it is capable. Stimulation of any part of the middle of the optic lobes or the medial, anterior, interbasal or lateral basal lobes will produce any of the responses that can be elicited by these methods from that lobe. This absence of localization presumably must have some limits, since there are specific tracts which have specific endings in the lower and intermediate motor centres. What these experiments indicate is that the cell bodies of these tracts are not aggregated together in discrete masses according to their function as von Uexküll's and Polimanti's observations implied. They are presumably spread out within any one lobe. The experiments do not show in what way these cells or aggregates of cells are distributed, or the nature of the contribution, if any, of the internuncial systems within the lobes.

I am most grateful to Professor J. Z. Young, F.R.S. for all the assistance he gave during this work, for allowing me to use his histological material and for reading the manuscript, also to Drs T. H. Bullock and R. W. Hunsperger for their critical comments. Most of the experimental work was done at the Stazione Zoologica, Naples, and my thanks are due to Professor R. Dohrn and Dr P. Dohrn and their staff for their very considerable help. Dr F. S. Russell, F.R.S. and his staff of the Marine Biological Association, Plymouth, where some of the final experiments were done, were similarly helpful. A grant from the Nuffield Foundation made the work possible. Mr J. Armstrong took the photomicrographs.

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Note added in proof 27 January 1961

Alexandrowicz has described the innervation of the hearts of *Sepia*, and shown that they are supplied both by fibres originating in the central nervous system and by fibres having their origin in the cardiac ganglion. (Alexandrowicz, J. S. 1960. Innervation of the hearts of *Sepia officinalis*. *Acta zool., Stockh.*, **41**, 65-100). He has also described a new muscle receptor organ situated under the nerves radiating from the stellate ganglion in *Eledone* (Alexandrowicz, J. S. 1960. A muscle receptor organ in *Eledone cirrhosa*. *J. Mar. biol. Ass. U.K.* **39**, 419-31).