The Structure and Connexions of the Corpora Pedunculata in Bees and Ants

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With two plates (figs. 3 and 6)

SUMMARY

1. A method is described of using high frequency radio waves to produce localized and precisely controlled burns. The technique is employed to damage the cells of the corpora pedunculata in bees and ants, and to follow the subsequent degeneration in these lobes.

2. The corpora pedunculata on each side of the brain are composed of four lobes: two calyces, an α lobe and a β lobe. Each fibre originates from a cell in the calyx, and has three branches, one to the calyx itself, one to the α lobe, and one to the β lobe. The arrangement of the tracts in these lobes is described.

3. The calyces and the α lobe both receive tracts from all the sensory centres of the brain, while the β lobe sends tracts to the motor regions. The detailed connexions of these tracts are described.

4. It is suggested that in the functioning of the corpora pedunculata the excitations from the calyx and the α lobe will interact, and that the excitation passing away down the β lobe is the result of this interaction.

INTRODUCTION

URING the past two years a physiological study has been made of the corpora pedunculata (mushroom bodies) in bees and ants. The superficial position of the cell-bodies in the central nervous system facilitated this study, which involved localized damage to the cells of the brain, followed by examination of subsequent degeneration. It is believed that the application of such a technique to invertebrates has seldom been attempted, and one object of this paper is to draw attention to the possibilities of the method. The use of this technique has enabled various assertions made by previous authors, on the basis of silver staining alone, to be re-examined.

Since the description of the 'corps pédonculés' by Dujardin (1850) these lobes have attracted much attention from microscopists. Papers by Kenyon (1896), Jonescu (1909), and Sanchez (1941) on the honey bee, and by Pietschker (1911) on the ant, are perhaps the most important contributions for the Hymenoptera. Thompson (1913) described various tracts within the mushroom bodies of ants, but the present study has failed to confirm many of her assertions, owing perhaps to her use of haematoxylin, which does not lend itself to detailed neurological studies. Hanström (1928) gives a survey of the older literature.

All these descriptions of the corpora pedunculata fall into two main groups: those dealing with the gross anatomy of the organ, and those concerned with minute details of individual neuron connexions. Between these two extremes lies what may be called the functional anatomy of the organ, dealing with a level of organization intermediate between the general form and the fine
detail. It is knowledge of precisely this level which was required in the present physiological study. This knowledge was unfortunately lacking, and, indeed, the detailed descriptions of the mushroom bodies already available, while important for some purposes, have tended to obscure the fundamental simplicity of their organization. The present paper attempts to remedy the deficiency and to give an account of the functional anatomy of the corpora pedunculata in bees and ants.

**Material and Methods**

The brain of the honey bee, *Apis mellifica*, and of the ants *Camponotus pennsylvannicus*, *Formica rufa*, *Eciton hamatum*, *Paraponera clavata*, and *Cryptocerus angulosus*, were examined; only the media workers were studied, and no attempt to compare either castes or species has been made. All the brains were stained by the silver-pyridine technique developed by Holmes (1947), which gave a consistently good result both for tracts and for individual axons. Two fixatives were found to be suitable: mercuric formaldehyde gave a good, rather bluish, stain with ants, while alcoholic Bouin gave a good reddish stain with bees.

The insects to be fixed were first anaesthetized with carbon dioxide, while the chitin overlying the brain was removed: this was found to be necessary to allow adequate penetration by the fixative. The toughness of the chitin precluded the regular preparation of a complete series of sections of the whole head, and the fixed brains were therefore dissected out before being embedded in the usual way.

In the experiments, in which the brains were intentionally damaged, two types of cautery were used. The first type was simply a nickel needle, of suitable size, heated to a dull red in the flame from a spirit lamp, and then placed immediately against the surface of the brain. With practice this gave fairly good results, and the method has the advantage of simplicity; there were, however, two serious disadvantages, both the result of lack of control of the heating effect: firstly, if the needle was too hot it seared the tissue for an ill-defined area around the point of contact, and, secondly, if the needle was too cold no damage was caused, and the operation was wasted.

It was obvious that what was required was a cautery, the power of which could be varied, and which would damage a well-defined and precisely controlled area. Such a cautery was constructed by utilizing the property of high frequency radio waves to produce burns when concentrated in a small area, while not harming a tissue in which they are dispersed. It is not proposed here to give details of the R.F. cautery which was constructed, for the same output could be achieved by a variety of different arrangements, all equally satisfactory, and indeed it is hoped to improve on the present apparatus. The output available was as follows:

- **Frequency**: 1.97 megacycles.
- **Max. power**: 25 volts.
- **Min. power**: 9 volts.
The most variable factor is the contact between the electrode and the tissue; a close, firm contact is essential for a good result. With the maximum power the damage produced made a small hole extending down from the electrode into the brain; with the minimum power the effect was only to coagulate the protoplasm of the cells with which the electrode made contact. The minimum power was therefore used when operating on the calyx, while the maximum power was employed in cauterizing the α lobe (see later).

The electrodes used were of platinum wire, insulated to the tip with glass. They were prepared by the method given by Johnson and Manhoff (1951). The area of damage to the brain coincided with the area of contact with the electrode; the diameter of the wire was therefore selected according to the amount of damage intended. For the success of the operation it was necessary that the insect should have a large capacity to earth: this was obtained by placing the abdomen in contact with an earthed metal plate.

The operating table was made of soft plasticine, moulded into a groove to fit the animal's body; the insect, with its head exposed, was then covered by another layer of plasticine over the thorax and abdomen. The bee or ant was thus held firmly by the plasticine which was, however, sufficiently yielding to prevent damage to the body or its appendages.

A series of exploratory dissections was done, and the various parts of the brain were localized with respect to various external features of the head. An experimental bee or ant was anaesthetized with carbon dioxide and placed on the operating table, which was set up on the stage of a dissecting microscope. A slit was made in the chitin of the head over the region to be cauterized. The electrode was then inserted until it was in contact with the surface of the brain, and the power switched on for 2–3 seconds; if a successful contact had been made the antennae usually twitched when the current was first switched on. The electrode was then removed and the slit in the head closed by flowing dental wax over the surface; this wax was eminently suitable for the purpose as it had a low melting-point, could be moulded easily with a warm needle, and formed a good joint with chitin. The operated insect was marked with cellulose paint for identification, and kept alive for several days. Degeneration was usually complete after 3 days from the time of operation. The brain was then fixed and sectioned as described.

A series of operations was done, both with bees and with all the species of ant listed. In the initial series the mushroom bodies on one side of the brain were completely destroyed, while in subsequent series the area of damage was progressively reduced until only small portions of the calyx were injured. The relatively small injuries were more easily produced on the bee's brain than on the ant's, owing to the larger size of the former, and for this reason the mushroom bodies of the bee have been studied in the more detail. So far, the damage has been restricted to the mushroom bodies themselves, but it is hoped to extend the study to other tracts and lobes of the brain. The use of electrodes insulated to the tip raises the possibility of causing damage deep in the brain—a technique which should give interesting results.
The general form of the corpora pedunculata

The corpora pedunculata in bees and ants are paired structures lying symmetrically on either side of the midline of the brain, and occupying the bulk of the protocerebrum. The structure on each side consists of a pair of fibrous calyces, which occupy the whole posteriodorsal region of the brain between the midline and the optic ganglia, and from which tracts descend to other regions of the brain. The rim of each calyx is roughly oval in shape: the medial calyx extends the further forwards, and overlaps the lateral calyx on the frontal surface of the brain, the condition being reversed on the lower surface where the lateral calyx extends further back. The cell bodies of the corpora pedunculata fill the calyces and slightly 'overflow' them. The rest of the structure is fibrous in nature and fairly sharply delimited from the rest of the brain tissue.

From each of the two calyces a short stalk, or pedunculus, extends downwards and forwards into the protocerebrum; the two stalks fuse with each other after a short distance and immediately after the point of fusion two other lobes are formed: the first of these passes forwards and upwards to the frontal surface of the brain, where it ends abruptly as a flat disk beneath the two or three layers of cell bodies which cover this region of the protocerebrum; the second lobe turns downwards and inwards and ends abruptly on the deep midline of the brain, where it abuts against the similar structure from the other side. The three lobes will here be referred to as the calyx, the $\alpha$ lobe, and the $\beta$ lobe, as shown in fig. 1. (See discussion below.)

All the nerve fibres constituting the corpora pedunculata originate from
cells within the bowl of the calyx. Each fibre has three branches, one to each of the three lobes, where they make synaptic connexions with incoming fibres from other parts of the brain. The calyx and the $\alpha$ lobe receive fibres from sensory centres, while the $\beta$ lobe gives connexions to fibres going to motor centres (see later).

The names of the various lobes of the corpora pedunculata have suffered from much confused variation. The terms 'calyx' and 'pedunculus' which are apt when applied to the Hymenoptera, and have the authority of long usage, will be used here; they would not be applicable to such orders as the Diptera, in which the equivalent of the calyx is a mere aggregation of cells (Bretschneider 1913; Power 1943). The other lobes have usually been referred to in English as 'roots', e.g. the anterior root and inner root of Kenyon (1896). The use of these terms has two disadvantages:

1. The word 'root' implies in its general sense both a source, or origin, and a means of attachment. In neither of these senses can the term be applied to the corpora pedunculata, for the fibres of this organ all originate in the calyx, and all end within the other lobes, making it a discrete structure, which is attached to the rest of the brain only by tracts originating in other parts of the brain, and most of which come to the calyx.'

2. The word 'root' is used in a specifically neural sense to designate those parts of peripheral, segmental nerves which lie immediately outside the central nerve cord. The 'roots' of the corpora pedunculata in no way resemble these.

Power (1943) has used the term 'stalk' in preference to 'root', following some other authors, but this does not resolve the problem, and indeed he is forced into the paradoxical situation of referring to the same structure both as a root and a stalk. It would seem preferable to avoid the use of botanical terms altogether, as Hanström (1928) and some other German authors may have tried to do by employing the terms 'rücklaufiger Stiel' and 'Balken': these terms still have some disadvantages, however, for in some insects, e.g. Drosophila, the 'Balken' appears more recurrent than the 'rücklaufiger Stiel'. It is also difficult to give a precise English translation of these two terms.

The three main subdivisions of the corpora pedunculata are in fact lobes, each with its own function, and it would seem desirable to refer to them as such. The lobes could then be further distinguished by reference to their relative positions, e.g. the upper lobe and the lower lobe, or the anterior and the posterior lobe. This would be unwise, however, for in different insects the apparently homologous lobes occupy very different positions: in the Lepidoptera and Hymenoptera, for example, the two homologous lobes ($\alpha$ lobe) run posteriorly and anteriorly respectively. In our present state of knowledge, therefore, it is preferable to give the lobes only general names which can be more precisely defined by future work in this field.

In the present work it is proposed to refer to the two lobes as the $\alpha$ lobe and the $\beta$ lobe respectively, as shown in fig. 1. This is preferred as the terms are indifferent as to structure, function, and orientation; thus one avoids confusion in comparative studies of orders in which the homologous lobes may
differ in all three factors. At the same time the general nature of the terms leaves the field clear for more precise definition in the future.

The relationships of the corpora pedunculata to the other lobes of the brain are shown in fig. 2. The relative sizes of the corpora pedunculata differ in different species of ants, being smallest in Eciton hamatum and largest in Formica rufa; this may be related to the fact that the eyes and optic ganglia

are small and degenerate in the Army ant, but large and well developed in the Wood ant (Werringloer, 1932). Goossens (1951), like other workers, has shown that the sizes of the mushroom bodies and the central body are inversely proportional, a fact which he attributes to the limited space available in the brain.

The fibres within the mushroom bodies are of two types, those originating within the organ and those arising from other association cells and connecting the mushroom bodies with the sensory and motor lobes of the brain. The fibres originating within the organ all arise from the cell-bodies in the calyces. According to Kenyon (1896) these neurons are all of one basic type: from each cell-body a projection passes down into the calyx where it divides into two parts, one forming arborescent synaptic connexions within the calyx, and

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**Fig. 2.** Frontal sections of the brains of the honey bee (*Apis mellifica*) and the Wood ant (*Formica rufa*).
undamaged medial calyx
degeneration in lateral calyx
median ocellus
degeneration in α lobe
degeneration in origin of α lobe
degeneration in lateral calyx

central body
degeneration in β lobe
degeneration in lateral calyx
degeneration in lateral calyx
oesophagus in lateral calyx
optic glomeruli

FIG. 3
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the other passing on down the pedunculus until it reaches the origin of the  
$\alpha$ lobe, where it bifurcates, sending one branch up this lobe and the other  
down the $\beta$ lobe, making synaptic connexions in both regions. The course of  
these fibres, provisionally established in silver preparations of normal material,  
has been confirmed in the present work, from the study of their degeneration.  
In fig. 3 is shown a series of sections of a bee's brain in which the lateral half  
of the lateral calyx has been cauterized; the degeneration can be seen passing  
from the calyx, down the pedunculus, and along the whole length of both the  
$\alpha$ and $\beta$ lobes. Detailed examination of such preparations reveals that the  
amount of degeneration remains fairly constant at all levels of the pedunculus  
and the lobes, which suggests that all the fibres extend for the whole distance.  
After leaving the calyx the degeneration also preserves its position relative  
to the circumference of each lobe, showing that the fibres do not deviate from  
their approximately straight course. The degeneration always ends within the  
mushroom body itself, which suggests that the fibres do not pass out into the  
mass of the brain; this should be particularly noted in reference to Thompson’s  
(1913) assertion that the tubercles of the central body are continuations of the  
$\beta$ lobe, for the degeneration never extends into these tubercles, neither does  
degeneration spread from one calyx into its neighbour, although Thompson  
also claimed that fibres take this course.

The association fibres from other parts of the brain pass in at the base of  
each calyx, and all round the sides of the $\alpha$ lobe and $\beta$ lobe. These fibres do  
not degenerate together with those of the mushroom body; in fig. 6, $B$ can be  
seen fibres from the optic ganglia passing through a degenerated region of the  
$\alpha$ lobe.

Tracts within the calyx

Most previous workers have noticed that the cells in the central region of  
each calyx stain more deeply with haematoxylin and silver than do the peripher-  
al cells. This has been confirmed in the present work, and the appearance  
of these cells is shown in figs. 3, 4, and 6, c. Thompson claimed that in  
*Camponotus pennsylvannicus* she could identify several groups of cells of  
different sizes across a single section of a calyx; these groups of cells have not  
been distinguished in my preparations. Fibres from the cells of the calyx are  
very fine, and have not stained individually or distinctly, except in a few  
cases. The fibres entering the corpora pedunculata, on the contrary, are fairly  
coarse and have stained clearly and precisely. In neither case, however, have  
fine terminations been seen, and it appears that Holmes’s stain is not suitable  
for such regions of these nerves. It is assumed that the synapses are of the  
arborescent type as described by Kenyon (1896) and confirmed by Sanchez  
(1941).

The fibres from the cell-bodies in the calyx pass directly outwards into  
the calyx wall. The fibres from the central group of cells stain more deeply  
than those from peripheral cells, and can be seen lying in a compact mass  
which forms a ring around the centre of the calyx. Degeneration studies show
that fibres run for a considerable distance around this 'central ring', often passing around to a point diametrically opposite to their place of entry. This is unlike the fibres from the peripheral cells, which do not pass far around the calyx.

The descending fibres from the peripheral cells are gathered into a series of radially arranged bundles, which become sharply defined as they pass downwards, and then turn horizontally inwards over the central ring, fuse with each other in the centre, and pass directly down through the ring into the pedunculus. Fibres from the central ring are not gathered into bundles, but pass directly inwards to the middle of the pedunculus and then turn down it.

The association fibres which enter the calyx from other parts of the brain do so at the junction of the calyx and the pedunculus. They then pass upwards, both inside and outside the central ring, to which they remain closely apposed, and pass around the calyx below the descending bundles, giving off branches into the peripheral region of the calyx and into the central ring. These afferent fibres form synaptic connexions with the fibres of the calyx itself, and Kenyon has recorded that a single afferent fibre may have connexions with many different calyx fibres.

**Tracts within the α lobe**

There are no separate tracts within the α lobe. The fibres coming from the pedunculus run straight along the lobe to its termination, and in sections transverse to its long axis it has a fairly homogeneous appearance. Association fibres from the rest of the brain enter over the whole of the surface, except at the extreme frontal tip. Tracts of association fibres which reach the surface immediately spread out and run around the lobe in both directions, sometimes

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**Fig. 4.** A diagram to show the arrangement of tracts within the calyx of *Apis mellifica.*
almost completely circumscribing it, and resembling in appearance a current of water eddying and swirling round a rock. Individual fibres are thus enabled to enter the lobe all around its surface; once inside they branch fairly profusely in all directions and run through the whole substance of the lobe, forming synaptic connexions with the mushroom body fibres. A typical arborescent fibre is shown in fig. 6, A. Sections at various levels of the lobe show a striated appearance, as in fig. 3, A. Kenyon claims that these striae are concentrations of synapses: if this is so then many association fibres must run along the length of the lobe for some distance, for at any one level the striae are restricted to one or two chords across the lobe, although the fibres spread out through the whole area.

**Tracts within the \( \beta \) lobe**

The appearance of the fibres within the \( \beta \) lobe is very similar to that described for the \( \alpha \) lobe above. The tracts of association fibres coming to this
lobe are, however, much fewer in number (see later), more diffuse, and run along rather than around the surface of the lobe, see fig. 6, c.

The association fibres which run along the surface of the lobe turn into it, branch, and synapse with the mushroom body fibres. Striations can again be seen, but they lie in bands parallel to the long axis of the lobe, rather than across it.

The connexions of the corpora pedunculata

The fibres of the corpora pedunculata all originate and end within the organ itself, which therefore depends entirely upon tracts coming from and originating in other regions of the brain. These tracts are of two types: those coming from the sensory centres, which all go to either the calyx or the \( \alpha \) lobe, and those going to motor centres from the \( \beta \) lobe. It is not proposed to describe the course of these numerous tracts in any detail, but merely to list them, together with a statement of their terminations. All the tracts will be referred to by numbers, and their correspondence with previously named tracts indicated where appropriate.

No detailed comparison of the insects studied has been attempted, for the amount of work involved would not be merited by the little we know either of true homologies in the insect brain or of the precise integrative functions of its lobes. The most notable difference between bees and ants is the large size of the optic glomeruli and their associated tracts in the former. Within the ants studied themselves the Army ant has degenerate optic glomeruli, and the tracts from them are insignificant. The brain of *Paraponera clavata* is very much larger than that of the other species, and is more easily studied, but the more common *Formica rufa* has been chosen for the type specimen here. However, the fundamental plan of the brain and its tracts is the same in all the species studied, which differ only in relative sizes and precise spatial relationships.

The numbers which have been given to the tracts indicate their order of appearance in frontal sections, starting with that nearest to the frontal surface of the protocerebrum. The size of the tracts has been exaggerated in the diagrams, and many of them (e.g. 6, 8, and 10 in fig. 7) have previously been referred to as bundles rather than as tracts; the latter term is used here for the sake of uniformity.

(A) The tracts in the honey bee

Tracts to the \( \alpha \) lobe

1. Passing between the two \( \alpha \) lobes. (Cell group I of Kenyon.)

2. From the inner optic glomerulus to the \( \alpha \) lobe, and then across to the opposite side of the brain, where it has the same connexions.

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Fig. 6 (plate), The fibres of various lobes of the corpora pedunculata of *Apis mellifica*.

A, section across an intact \( \alpha \) lobe.

B, section across a partially degenerated \( \alpha \) lobe.

C, section through a calyx, corresponding to fig. 5, section 7.

D, section through the upper surface of the \( \beta \) lobe.

All the sections are frontal; in each case the dorsal side is turned towards the right side of the plate.
"central ring"

central cell group

fibres to central body

arborescent neuron entering α lobe from protocerebrum

body of α lobe

undegenerated afferent fibres

degeneration in fibres of corpora pedunculata

FIG. 6
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3. From the optic tubercle to the α lobe. (Cell group V of Kenyon.)
4. From the inner optic glomerulus to the α lobe.
5. From the middle optic glomerulus to the α lobe. This tract has three origins: one from the middle region of the glomerulus and one each from the upper and lower surfaces.

6. From the outer side of the antennal glomerulus to the α lobe. (Cell group VII of Kenyon.)
7. From the optic tubercle to the α lobe. (Cell group IV of Kenyon.)
8. From the middle inner surface of the antennal glomerulus to the α lobe. (Cell group VII of Kenyon.)
9. From the inner optic glomerulus to the α lobe.
10. From the middle inner surface of the antennal glomerulus to the α lobe. (Cell group VII of Kenyon.)
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11. From the optic tubercle to the α lobe.
12. From the suboesophageal region to the α lobe.

**Tracts to the calyces**

I. From the optic tubercle to the calyces.
II. From the antennal glomerulus to the lateral calyx. (The outer antennal-glomerular tract of Kenyon.)
III. From the inner optic glomerulus to the calyces.
III'. From the inner optic glomerulus to the calyces, but passing below the pedunculi and originating lower in the optic glomerulus. (The posterio-superior optic tract of Kenyon.)
IV, V, and VI. From the middle optic glomerulus to the calyces. (The antero-superior optic tract of Kenyon.)
VII. From the suboesophageal region to the calyces. (The dorso-ventral tract of Kenyon.)
VIII. From the antennal glomerulus to the medial calyx. (The inner antennal-glomerular tract of Kenyon; the tractus olfactorio-globularis of Hanström.)
IX. From the suboesophageal region of the opposite side to the lateral calyx.
X. From the suboesophageal region of the same side to the lateral calyx.

**Tracts from the β lobe**

a. Coarse fibres passing from the β lobe to the central complex beneath the central body. These are not gathered into a well-defined bundle.
b. From the β lobe to the antennal-motor centre.
c. From the β lobe to the suboesophageal region of the same side.
d. From the β lobe to the suboesophageal region of the opposite side.

(B). The tracts in the ant *Formica rufa*

**Tracts to the α lobe**

1. Passing between the two α lobes.
2. From the inner optic glomerulus to the α lobe.
3. From the optic tubercle to the α lobe.
4. From the middle optic glomerulus to the α lobe.
5. From the suboesophageal region to the α lobe.
6. From the antennal glomerulus to the α lobe.

**Tracts to the calyces**

I. From the optic tubercle to the calyces.
II. From the antennal glomerulus to the lateral calyx.
III. From the inner optic glomerulus to the calyces.
IV. From the antennal glomerulus to the lateral calyx.
V. From the middle optic glomerulus to the calyces.
VI. From the suboesophageal region to the medial calyx.
VII. From the suboesophageal region to the lateral calyx.
VIII. From the antennal glomerulus to the medial calyx.
IX. From the antennal glomerulus to the lateral calyx.
X. From the antennal glomerulus to the lateral calyx.
XI. From the suboesophageal region to the lateral calyx.
XII. From the antennal glomerulus to the lateral calyx.

Fig. 8. Diagrams to show tracts connecting the corpora pedunculata with the rest of the brain in Formica rufa. The numbers of the frontal sections in which the tracts appear are shown below each picture. For description see text.

\( o.t. = \) optic tubercle,
\( a.m. = \) antenno-motor centre.

Tracts from the \( \beta \) lobe

\( a. \) From the \( \beta \) lobe to the central complex, beneath the central body.
\( b. \) From the \( \beta \) lobe to the antenno-motor centre.
\( c. \) From the \( \beta \) lobe to the suboesophageal region of the opposite side.
\( d. \) From the \( \beta \) lobe to the suboesophageal region of the same side.

In view of Power's (1946) criticism of Sanchez's (1941) term 'antenno-motor centre' it should be stated that the present study both confirms and extends the latter author's observations. Unlike the situation in Drosophila the major part of the antennal nerve does enter the antennal glomerulus in the
honey bee and in ants. The fibres which pass by the morula are of two sorts: numerous large, coarsely-staining motor fibres which pass on the ventrolateral side of the morula to the fibrous structure called the antenno-motor centre; and much fewer lightly staining fibres which pass below the morula to its medial, inner side, and end in a few glomerular bodies resembling those of the true morula. In the above account the antennal glomerulus is taken to include both the morula-like lobes: their tracts can be distinguished from that to the motor centre. A commissure of the motor lobe has been distinguished passing just above the oesophageal foramen, and this implies that the lobes are of a deuto cerebral nature, unlike the similar structures in Drosophila. The present study differs from that of Sanchez in distinguishing between the tract from the β lobe to the antenno-motor centre, and the tracts from the cells of the glomerulus to the medial calyx (A, VIII, the olfactorio-globularis): the two tracts are not the same, as Sanchez suggests.

Several of the tracts listed above are shown to come from the suboesophageal region, but their origins here have not been traced: Kenyon has shown that some of the fibres from the β lobe make connexions with those from the thoracic ganglia. So little is known of the neurology of the suboesophageal ganglia that there is no other indication whether the fibres to the protocerebrum come from sensory or motor areas. The following considerations are however relevant here:

1. Tracts from the optic glomeruli and the antennal glomeruli, all of which are sensory centres, go only to the calyces and the α lobes.
2. Tracts from the β lobes go to the antenno-motor centre and the central body. The central body itself also receives tracts from all the sensory centres and is intimately connected with the suboesophageal ganglia.
3. The suboesophageal ganglia, apart from their role as centres for the mouthparts, have important functions in maintaining locomotor activity in the insect.

It therefore seems reasonable to suppose that the tracts from the suboesophageal ganglia to the calyces and α lobe are from sensory areas. It is further suggested that tracts from the β lobe are to motor regions; which implies that the central body has motor functions, although there is no physiological evidence on this point. These topics will be further discussed in the next section.

**Discussion**

Since the mushroom bodies were first described, over a century ago, their function has been the subject of much speculation: all the fashionable mysteries of behaviour have been successively attributed to them. It is not proposed to add to these speculations here, but only to discuss the manner of functioning which their anatomical properties may confer upon them.

The descriptions given make it clear that the calyces and the α lobe both receive connexions from all the sensory centres of the brain. Although the
fibres entering the calyces and \( \alpha \) lobe have not been counted, it is obvious that they are very numerous, and this, allied with the fact that a single afferent fibre makes synaptic connexions with many mushroom body fibres, makes it probable that each of the latter fibres has at least two connexions with sensory centres—one in the calyx and one in the \( \alpha \) lobe. Although there is no evidence that the insect synapse is polarized, it seems more probable that the flow of excitation is from the sensory centres into the corpora pedunculata rather than the reverse. If this is so, then when the sensory centres are active each of the mushroom body fibres will be simultaneously excited both in the calyx and in the \( \alpha \) lobe. If the two excitations are not synchronized, then the excitation which passes away down the \( \beta \) lobe must be the result of a combination or interaction of the two initial excitations in the calyx and \( \alpha \) lobe. The possession of two reception areas, each with duplicate connexions, thus introduces the possibility of a type of comparator system which can be used to produce great variation in the transmitted information; this variation being caused by excitations arising in either the same or in different sensory centres. The mechanism for producing this variation will be discussed elsewhere.

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**Fig. 9.** Diagram to illustrate the suggested paths of conduction in the corpora pedunculata.  
\( S_1 \) and \( S_2 \) = sensory centres.  
\( M \) = motor centre.
The hypothesis given above is not the only one which would explain the facts. If, for example, it was supposed that tracts from the $\alpha$ lobe conducted excitation away from the lobe to the sensory centres, then some sort of self-exciting circuit might be set up, involving the series sensory centre $\rightarrow$ calyx $\rightarrow$ $\alpha$ lobe $\rightarrow$ sensory centre $\rightarrow$ &c., with a continual excitation passing away down the $\beta$ lobe. Until some evidence is available to show that integrative centres may react upon sensory centres, it seems wiser, however, to assume that the flow of excitation normally passes from the sensory centres to the mushroom bodies, with the results already proposed.

If, as suggested, the $\beta$ lobe is a transmitting region, then it is clear that tracts from this lobe must conduct excitation away to motor or integrative centres, as has already been suggested in discussing the origins of these tracts.

The polysynaptic connexions and large number of the fibres entering the calyx make it probable that the afferents must compete for the mushroom body fibres, which thus exemplify the 'convergence' and 'final common path' postulated for other neural organizations. If one afferent fibre can excite several post-synaptic fibres, then the calyx will act as a primitive amplifier. Perhaps more important, however, is the increased probability that in a population of post-synaptic fibres with varying thresholds at least a few will always be excited by the afferent impulse. This implies that on different occasions the same afferent fibre excites different post-synaptic fibres, which raises the question of the degree of localization of function, if any, which exists in the calyx. On anatomical grounds one might expect the different calyces, and the central and peripheral groups of cells within each calyx, to have different functions. The arrangement of the synaptic striae across the $\alpha$ lobe and along the $\beta$ lobe, together with the observation that all the mushroom body fibres rigidly preserve their relative positions in these lobes, might indicate that the spatial distribution of the fibres has some functional significance. Any final determination of the functional localization must, however, depend upon physiological rather than histological observations.

It is indeed apparent that although we have a detailed knowledge of the histology of the corpora pedunculata, our ignorance of their function remains very great. Only physiological examination can clarify this matter, but it should be stressed that comparative studies of a physiological and a histological nature are complementary, and both are essential to a further understanding of the problem.

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