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Organization of sensory-motor lobes in the brain of *Octopus vulgaris*.

I. Central afferent and efferent pathways of suboesophageal nerves

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The paper is dedicated to the memory of Professor John Z. Young, F.R.S., F.B.A.

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CONTENTS

SUMMARY

Centripetal cobalt fillings have shown many new efferent and afferent pathways in the *Octopus* brain, in addition to those found earlier by anatomical studies and degeneration (Young 1971). These new findings show that the innervation of the complex muscle systems of these animals involves a distribution of motoneurons that is different from that found in either vertebrates or arthropods.

There is much overlap of efferents projecting to different effector systems. An area in the anterior pedal lobe that gives rise to the efferents to the brachial nerves overlaps with the areas of the head and funnel nerve efferents, which reach to the posterior pedal (head nerves) and palliovisceral lobes (funnel nerves). The head and funnel nerve efferents overlap with the efferents of the inferior and posterior superior ophthalmic nerves; the area of overlap includes parts of the posterior pedal, palliovisceral and ventral magnocellular lobes. The efferents of the pallial nerve in the palliovisceral and posterior ventral magnocellular lobes are adjacent to the efferents of the head nerves and overlap with those of the funnel, ophthalmic and statocyst nerves and with the efferents of the brachial nerves in the magnocellular lobe. The statocyst efferents in the ventral magnocellular, lateral anterior palliovisceral and lateral pedal lobes also overlap with efferents of the oculomotor nerves in the anterior lateral pedal lobe. Here, in the anteroventral part of the anterior lateral pedal lobe, efferents of all the effector systems overlap.

In all the suboesophageal brain areas mentioned above, the efferents are not somatotopically arranged. Within the zones of overlap, the collaterals of efferents of different nerves overlap and form almost orthogonal meshworks.

The data for the afferents in the various nerves also show many interesting new features. Afferents of the arm, head, mantle and statocyst nerves converge in five overlapping regions (figures 60-62): (i) in the prebrachial lobes at the level of the infrabrachial commissure; (ii) in the centre of the brachial lobes; (iii) in the continuous posterior lateral pedal, median basal and precommissural lobes; (iv) in the anterior ventral magnocellular lobe; and (v) in the posterior ventral magnocellular lobe. Throughout all motor output regions afferent input occurs from peripheral nerves.

The results offer a new description of the outlines of the palliovisceral, magnocellular and lateral pedal lobes and provide a deeper insight into the intermediate/lower motor concept and the difficulties that occur when applying that concept to the organization of the cephalopod brain. The differences and similarities of the sensory-motor organization of *Octopus*, insects and vertebrates are discussed.

1. INTRODUCTION

The position and function of the motor centres in the brain of cephalopods are well known (*Sepia*: Boycott 1961; Chichery & Chanelet 1976, 1978; Chichery 1983; Messenger 1983; *Lolliguncula*: Novicki et al. 1990; *Octopus*: Messenger 1967a,b; Young 1971; Wells 1978). Based on the interpretation of lesion and stimulation experiments they have been classified into lower, intermediate and higher motor centres (Sanders & Young 1940; Boycott 1961; Young 1971; Wells 1978; Messenger 1983). Electrical stimulation of lower motor centres results in movements of solitary groups of muscles. Stimulation of intermediate motor centres elicits movements of whole groups of muscles. Stimulation of higher motor centres causes complete behavioural motor patterns; these are characterized by a coordinated and frequently sequential activation of several groups of muscles. In addition, stimulation of the optic lobes may elicit a still greater variety of graded and coordinated behavioural patterns or even whole sequences of them. This variety may reflect the dependence of cephalopod behaviour on the instruction of varying visual inputs; therefore, these lobes have been called "controlling centres" (Young 1976; Messenger 1983).

The central nervous pathways of the tracts and nerves that are involved in motor responses are partly known. In *Octopus vulgaris*, they have been described for the statocyst and extraocular eye muscle nerves and for the arm and mantle nerves by means of cobalt and HRP filling and staining techniques (Budelmann & Young 1984, 1985; Saidel & Monsell 1986). The perikarya of the motoneurons of the seven extraocular eye muscle nerves are located in the anterior lateral pedal lobe; two of the nerves have perikarya also in the transition region of the magnocellular and posterior pedal lobes. Many motoneurons of the pallial and brachial nerves have been shown to originate in the anterior and posterior chromatophore and in the magnocellular and palliovisceral lobes. Further efferents of the brachial nerves originate in the prebrachial, brachial and anterior pedal lobes. The suboesophageal pathways of the head and body motor nerves (antorbital, interbrachial, head retractor, funnel, medial pallial retractor, collar, and visceral nerves), as well as pathways from the optic lobes and higher motor centres, have been analyzed from degeneration experiments (Young 1971). This method, however, does not allow description of the origin and proximal part of their motoneurons. A few connections from the optic lobes to the peduncle, lateral basal and perhaps magnocellular lobes have been described by means of HRP (Saidel 1981, 1982).

The aim of this present work is to provide more details about the central nervous pathways of the head and body motor nerves of *Octopus*, using centripetal cobalt fillings; in contrast to results from degeneration, this technique allows description of also the origin and proximal part of the motoneurons. Together with data already known for the brachial, pallial, eye muscle and statocyst nerves (Colmers 1982; Budelmann & Young 1984, 1985; Saidel & Monsell 1986), these allow revision of the functional organization of the suboesophageal motor centres and finally discussions

of these centres in more general and comparative terms. The present work is the first of three papers on the brain of *Octopus* that focus on the functional neuroanatomy of its sensory-motor lobes. The other two papers will describe the interneuronal connections of the suboesophageal, perioesophageal, supraoesophageal and optic lobes (Plän & Budelmann - a & b, in preparation).

2. MATERIALS AND METHODS

82 *Octopus vulgaris* were used in this study. They were obtained from either the Gulf of Naples (75 animals of 100-400g, males and females) or the Catalonian Sea (seven animals of 600-1000g, males). Most experiments were done at the University of Regensburg, where the animals were kept separately in tanks (20 liters) in a closed circulation of artificial seawater at 12-18°C. Few additional experiments were done at the Stazione Zoologica (Naples, Italy) and the Laboratoire Arago (Banyuls, France).

Centripetal cobalt fillings were done with the following nerves (for terminology see Young 1971): superior and inferior antorbital, interbrachial, anterior and posterior head retractor, anterior and posterior funnel, medial pallial retractor, collar, pallial, fourth brachial, inferior ophthalmic, posterior root of the posterior superior ophthalmic, medial and posterior crista, macula, and visceral nerves. In nine animals, fillings were also done with branches of the anterior oculomotor, middle superior ophthalmic and anterior funnel nerves. The experiments were performed on isolated head preparations with the nerves of both the left and right side. The nerves were dissected from their surrounding tissue and cut 2-3 mm before entering the brain. For the routine procedure of the cobalt filling technique and subsequent histological treatment see Budelmann & Young (1984, 1985).

For each nerve at least two fillings were done. For a reconstruction of the topographical organization of the suboesophageal brain, the preparations were serially sectioned at 40 μm, one in a transverse and one in a sagittal plane. The material of Budelmann & Young (1984, 1985) has been reexamined and some of it has been additionally used in this analysis. For additional information about the relative position of the motoneurons and afferent fibres, a few fillings were done with two nerves simultaneously. Since the double-staining technique with nickel and cobalt (Quicke & Brace 1979) did not give useful results, cobalt solutions of different molarity (1.0 M and 0.2 M) were used. This technique results in dark and lightly stained cells and fibres and this difference remains also after intensification. In a few instances, dark and lightly stained neurons occurred in fillings of just one nerve. This might be due to cobalt-coupling (Strausfeld & Obermayer 1976; Strausfeld & Bassemir 1983). Units were called "secondarily filled" only if their lightly stained fibres could be traced back to the presumptive coupling sites with primarily dark stained fibres.

The diameters of the perikarya were classified into very small (<10 μm), small (10-20 μm), medium (20-40 μm), large (40-60 μm) and very large (>60 μm) (see Budelmann & Young 1984). All counts of perikarya are given in approximate minimum numbers. The diameters of afferent fibres were classified into very fine (<<1 μm), fine (<1 μm), medium (1-5 μm) and large (>5 μm). The terminology of the *Octopus* central nervous system is based on Young (1971) (see also figure 14). If not otherwise stated, the designated c.n.s. areas are ipsilateral; in some instances, the abbreviation "i./c." was used for "ipsi- and contralateral".

Note. For references to figures of afferent and efferent fibres of a given nerve, there is a distinction between "(figure 00)" and "(see figure 00)". As indicated in the figure legends, the latter refers to data of a different nerve but with similar fibre distribution. There is also a distinction between efferents, motoneurons and efferents/motoneurons. "Efferents" is used as a collective term for all output fibres. "Motoneurons" is used for motor output fibres, i.e. fibres that directly innervate muscles that contract after stimulation of the site of origin of the neurons (Boycott 1961). The term "motoneuron" is also used for fibres of the brachial and pallial nerves that are pre-motor to the motoneurons in peripheral ganglia (Graziadei 1971; Lund 1971). Finally, "efferents/motoneurons" is used whenever it is not completely clear whether all the efferents are exclusively motoneurons. A further distinction is made between interneuron and local neuron. Here "interneuron" is used for a neuron that connects two different lobes, whereas "local neuron" is used for a neuron that is intrinsic to a lobe, i.e. has an axon and dendrites that do not leave its lobe.

3. RESULTS

(a) *Organization patterns of the suboesophageal neuropil*

In most suboesophageal lobes, the trunks of several perikarya often join side by side and form "fibre channels" that then proceed radially into the neuropil. In the prebrachial, brachial, pedal, palliovisceral and magnocellular lobes, these fibre channels become evident at entry into the neuropil, whereas in the chromatophore and vasomotor lobes they are clearly visible already within the perikaryal layers. Each channel contains between four and more than 100 fibres; larger channels are frequent in the chromatophore and vasomotor lobes and often also contain input fibres that proceed into the perikaryal layers. The distance between two neighbouring channels differs, but is generally between 30 and 200 μm. Within the neuropil, a single trunk may leave its channel and join another, usually neighbouring one; the extent of this interchange differs in the different lobes. At short intervals, single collateral fibres, at longer intervals bundles of them, branch off from the trunks orthogonally and may cross several fibre channels. Collaterals of different neurons and different fibre channels often run parallel and form loose fibre layers (figure 29). Together with bundles of input fibres, they form nearly orthogonal fibre meshworks. These are most obvious in

the chromatophore lobes, where the fibre bundles are uniform in diameter and similar in distance to each other (see Young 1971). These meshworks, as well as fibre channels, are absent in the funnel lobes, the interbrachial lobules and the posterodorsal lobe.

(b) ***Borders of some suboesophageal lobes***

In the past exact outlines of some suboesophageal lobes remained somewhat unclear (see Young 1971). They can now be redefined according to the present cobalt findings. In addition, some lobes can be divided into anatomically distinct parts.

(i) *The posterior lateral pedal lobe*

This lobe can be subdivided into an anterior and a posterior part (figure 26). The anterior part bulges laterally as does the anterior lateral pedal lobe. Ventrally its neuropil is delineated at its anterior border by the most anterior fibres of the statocyst's macula nerve and at its posterior border by the most posterior fibres of the statocyst's crista nerves (figure 59). Dorsally the lobe is continuous with the most posterior part of the anterior basal lobe. The posterior part of the posterior lateral pedal lobe lies at the level where the lateral surface of the suboesophageal brain forms a groove surrounded anteriorly by the anterior part of the posterior lateral pedal lobe, posteriorly by the dorsal magnocellular lobe, dorsally by the interbasal lobe, and ventrally by the anterior ventral magnocellular lobe; its front end lies immediately behind the incoming anterior crista nerve. Together with the anterior ventral magnocellular lobe beneath, it neighbours the posterior part of the posterior pedal lobe. Its neuropil is crossed by the brachial-optic lobe tract. The posterior part of the posterior lateral pedal lobe is anterior to the anteroventral part of the dorsal magnocellular and the dorsal part of the middle ventral magnocellular lobes; with them, however, there is no fibre exchange. At the level of the interbasal lobe and the suprapedal commissure its neuropil becomes confluent dorsally with that of the precommissural and median basal lobes. The significance of the two subdivisions of the posterior lateral pedal lobe will be discussed in the second paper of this series (Plän & Budelmann - a & b, in preparation).

(ii) *The ventral magnocellular lobe*

This lobe can be subdivided into anterior, middle and posterior parts (see also Young 1971). The anterior ventral magnocellular lobe (figure 26) encloses the brachio-palliovisceral connective, which gives off the brachial-optic lobe tract at this level. The lobe flanks the posterior half of the posterior pedal lobe. Its posterior boundary is marked by a layer of perikarya that separates the lobe medially from the posterior pedal lobe. The anterior ventral magnocellular lobe has no dorsal perikaryal layers.

The middle ventral magnocellular lobe (figures 38 and 55) is confluent with the lobe's anterior part. Its dorsal perikaryal layers neighbour the dorsal magnocellular neuropil on the medial side. The lateral perikaryal layers of the two lobes are separated by a well-marked groove (see figure 6.3 of Young 1971). The middle ventral magnocellular lobe encompasses the passing through bundles of the broken-up brachio-palliovisceral connective and flanks the anterior palliovisceral lobe. Posteroventrally, its boundary is marked by the inner edge of the posterior funnel lobe, anterodorsally by the internal median basal-palliovisceral lobe tract and posterodorsally by the neuropil that connects the posterior chromatophore and palliovisceral lobes.

The posterior ventral magnocellular lobe (figures 35, 41 and 46) joins the lobe's middle part behind the posterior funnel lobe and the posterior chromatophore-palliovisceral neuropil connection. It lies beneath the posterior chromatophore lobe and flanks the posterior palliovisceral lobe (see below). Ventrally, the posterior ventral magnocellular lobe occupies the region anterior to the magnocellular commissure (see below), i.e. the ipsi- and contralateral lobes are ventrally continuous. Its neuropil is partly confluent with that of the ventrolateral vasomotor lobe.

According to the lobe borders described, the middle and posterior ventral magnocellular lobes include brain regions which were previously thought to belong to the palliovisceral lobe; (e.g. the middle and posterior palliovisceral commissures, see Young 1971; Budelmann & Young 1985).

(iii) *The posterior magnocellular lobe*

This lobe is the posteroventral continuation of the dorsal magnocellular lobe. Their neuropils and perikaryal layers show the same features. The posterior magnocellular lobe flanks posterolaterally and, by the magnocellular commissure, posteroventrally the posterior part of the ventral magnocellular lobe (figure 35).

(iv) *The palliovisceral lobe*

This lobe can be subdivided into an anterior and a posterior part (figures 41-44). The front end of the anterior part lies behind the layer of cells between the anterior ventral magnocellular and the posterior pedal lobes. Laterally, it is flanked by the middle ventral magnocellular lobe. The posterior margin of the anterior part is marked by the intervasomotor tract. The posterior part of the palliovisceral lobe joins the anterior part dorsally. It lies posterior to the neuropil connection between posterior chromatophore and palliovisceral lobes and dorsally and medially posterior to the posterior part of the ventral magnocellular lobe. Posteriorly it joins the medial dorsal vasomotor lobe (figure 45). There are no ventral perikaryal layers.

(c) ***Efferent and afferent pathways of suboesophageal nerves***

A detailed description will be given of the afferent and efferent pathways of the superior and inferior antorbital, interbrachial, head retractor, medial pallial retractor, anterior and posterior funnel, collar, and visceral nerves. Some new findings will be added to the available data of the brachial, pallial, extraocular eye muscle, and statocyst nerves. For each nerve, the first paragraph will briefly summarize respectively the origin and termination of these fibres, and the following paragraphs will give the details. Within the brain the nerves divide into distinct bundles that can be followed individually along their course through the brain; for the purpose of description and later references, they were labeled with roman numerals. Some fibres are difficult to assign to one or the other bundle, and this will be indicated by a question mark together with the numeral.

(i) *Superior antorbital nerve*

The superior antorbital nerve enters the suboesophageal brain dorsolaterally behind the first brachial nerve. At entry it divides into six distinct bundles (I-VI). Their efferents originate in the interbrachial lobule 1 (II), the prebrachial (I), anterior pedal (V), anterior lateral pedal (V), anterior chromatophore (VI), and superior buccal (I) lobes. The afferents run to the interbrachial lobule 1 (II), the prebrachial i./c. (I, II), brachial i./c. (I or II), anterior ventral magnocellular (II, IV), posterior part of the posterior lateral pedal (III), posterior pedal (III), superior buccal (I), posterior buccal (I), and median basal (III) lobes (figure 1).

Bundle I contains both efferent and afferent fibres. Some pass to suboesophageal and others to supraoesophageal parts of the brain. The suboesophageal efferents originate from about 60 medium perikarya dorsally in the prebrachial lobe. There, two or more of their trunks may enter the neuropil close together within one fibre channel.

The suboesophageal afferents are mainly varicose and fine or medium. Some pass to the contralateral side of the brachial lobes through the corridor of either the infrabrachial commissure beyond the fourth brachial nerve, or the suprabrachial commissure to the area of the first and second brachial nerve (figures 15 and 16; see also figures 22 and 25). The afferents in the corridor of the infrabrachial commissure are possibly accompanied by fibres of bundle I efferents. Other supraoesophageal afferents pass through the brachial-buccal lobe tracts of the cerebro-brachial connective to enter the superior buccal and the anterior part of the posterior buccal lobes. There, they run parallel to the edge of the neuropil and end in various depths (figure 16). The supraoesophageal efferents arise from small perikarya in the lateral aspect of the superior buccal lobe and pass through the brachial-superior buccal lobe tract (figure 16).

Bundle II also contains afferent and efferent fibres. They run anteriorly in the nerve and enter, together with bundle I of the first interbrachial nerve, a dorsal protrusion of the prebrachial lobe, the interbrachial lobule 1 (see § 3.c.iii). The efferents originate here from small and medium perikarya which also contribute to the first interbrachial nerve. The afferents pass through the lobule, crossing the trunks of the efferents at various angles, and join the afferent fibres of bundle I in the infrabrachial commissure where they presumably end. Some fine afferents pass through the lateral perikaryal layer of the anterior brachial lobe and enter, together with bundle IV afferents, the brachio-palliovisceral connective; they terminate in the anterior ventral magnocellular lobe. Some single mainly fine afferents can be seen crossing the dorsal brachial lobe to the contralateral side.

Bundle III contains only fine afferent fibres. They run to the posterior pedal and posterior part of the posterior lateral pedal lobes. There, the bundle divides into three branches that break up (i) in the posterior lateral pedal and adjacent dorsal posterior pedal lobes, at the level of the brachial-median basal lobe and brachial-optic lobe tracts, (ii) along the ventromedian border of the anterior part of the posterior pedal lobe, and (iii) ventro-anteriorly in the continuous neuropil of the precommissural and median basal lobes, at the level of the suprapedal commissure (figure 23; see also figure 24).

Bundle IV contains 10-20 medium afferent fibres. They run close together with fibres of the first brachial nerve into the brachio-palliovisceral connective to terminate in the anterior ventral magnocellular lobe (see figure 26).

Bundle V contains only efferent fibres. They originate from 150 large perikarya in three brain regions of the anterior pedal and anterior lateral pedal lobes: (i) 30 perikarya in the anteroventral part of the anterior lateral pedal lobe, immediately behind the anterior chromatophore lobe and above the brachio-palliovisceral connective, (ii) 50 perikarya dorsolaterally in the anterior pedal lobe, posterior to the entry of the anterior root of the posterior superior ophthalmic nerve, and (iii) 70 perikarya ventrolaterally in the anterior pedal lobe, posterior to the entry of the inferior antorbital nerve. The trunks of all these efferent neurons usually enter the neuropil one per fibre channel (figure 21; see also figures 17, 18 and 20).

Bundle VI contains efferent and few probably afferent fibres. The efferents originate from 60 medium perikarya in the posterior two third of the anterior chromatophore lobe (see figure 19). Fine fibres, probably afferents, run into the interchromatophore connective, but none were seen reaching the posterior chromatophore lobe.

(ii) *Inferior antorbital nerve*

The inferior antorbital nerve enters the brain ventrally at the anterior edge of the anterior pedal lobe and medial to the brachio-palliovisceral connective. It divides into five bundles (I-V). Their efferents originate in the anterior chromatophore (V), anterior pedal (IV), and anterior lateral pedal (IV) lobes. Their afferents run to the prebrachial i./c. (I), brachial i./c. (I), anterior ventral magnocellular (III), posterior part of the posterior lateral pedal (II), posterior pedal (II), and median basal i./c. (II) lobes (figure 2).

Bundle I contains afferent fibres. They run forward through the brachio-palliovisceral connective to enter the brachial lobe. Single fine and medium fibres can be traced within the ipsi- and contralateral brachial lobe. Most fibres spread into the prebrachial lobe and some pass to the contralateral side through the corridors of the infra- and suprabrachial commissures (figure 25; see also figure 22).

Bundle II also contains afferent fibres. They run dorsally backwards in the brachio-palliovisceral connective and leave it at the level of the brachial-optic lobe tract. They terminate in three lobes: (i) the posterior part of the posterior lateral pedal lobe, with very fine varicose fibres dorsally and single fine fibres ventromedially, (ii) the lateral parts of the posterior pedal lobe, and (iii) mainly anteriorly in the continuous neuropil of the precommissural and ventral median basal lobes, with fibres crossing through the suprapedal commissure to the contralateral side (figure 24; see also figures 23 and 26).

Bundle III also contains only afferent fibres. They run through the brachio-palliovisceral connective into the anterior ventral magnocellular lobe (see figure 26) and distribute in longitudinal and vertical directions in various depths of this lobe.

Bundle IV contains efferent fibres. They originate from 240 medium and large perikarya in the pedal lobes: in the anterior pedal lobe, 120 perikarya dorsally (figures 17 and 18) (some varicose fibres occur here also and might be afferent) and 60 perikarya ventrally, in the anteroventral part of the anterior lateral pedal lobe, 60 perikarya anteriorly (figure 20). These areas of origin match with those of the efferents of bundle V of the superior antorbital nerve, but the inferior antorbital nerve has additional perikarya postero-medially in the anterior pedal lobe. 70 perikarya, secondarily filled in the confluent neuropil of the anterior pedal and anterior lateral pedal lobes, are stained in the more posterior part of the anterior lateral pedal lobe, with medium and large perikarya in the middle and outer perikaryal layers (figure 20); their fibres make contacts deeply in the continuous anterior pedal / anterior lateral pedal neuropil.

Bundle V also contains efferent fibres. They originate from 90 medium perikarya in the anterior chromatophore lobe and are mainly located in the outer perikaryal layers of the posterior two third of this lobe (figure 19). One to five trunks of these neurons run inside each fibre channel. Varicose fibres cross their trunks at various depths. Some very fine fibres run into the interchromatophore connective, but none were seen reaching the posterior chromatophore lobe; these fibres might be afferent, but there nature is uncertain.

(iii) *Interbrachial nerves*

There has been confusion about the nomenclature of the nerves that run beside the four brachial and two antorbital nerves. Thore (1939) called the nerves beside the second and fourth brachial nerves "nervi interbrachiales" and those beside the first and third brachial nerves "nervi musculares". He described the "nervus antorbitalis inferior" as being anterior to the "nervus muscularis inferior"; Young (1965) mentioned interbrachial nerves along the first and second brachial nerves, and Young (1971) described the "nervi musculares" as included in the antorbital nerves (i.e. beside the first and third brachial nerve). Young's (1971) description of the central nervous pathways of the inferior antorbital nerve is identical with that of Thore`s (1939) "nervus muscularis inferior".

The two "nervi interbrachiales" and two "nervi musculares" clearly run beside the four brachial nerves. They innervate consecutively the pillar-muscles ("Pfeiler-Muskel", Pfefferkorn 1915) between the bases of the arms. Moreover, since the fibres of these four nerves all originate, or terminate, in the same brain regions, it is more appropriate to call these nerves "interbrachial nerves 1, 2, 3 and 4". Contrary to Thore (1939), the interbrachial nerve 3 (described as "nervus muscularis inferior") enters the brain anterior to the inferior antorbital nerve. The present results for the four nerves are basically similar and data will be given for a single nerve; differences between the four nerves will be outlined.

After entry into the prebrachial lobe, each interbrachial nerve divides into four bundles (I-IV); the interbrachial nerve 1 forms an additional fifth bundle (V). Efferents of the interbrachial nerves originate in their respective interbrachial lobules (I), the anterior chromatophore (V), anterior pedal (IV), and anterior lateral pedal (IV) lobes. Afferents run to the respective interbrachial lobules (I), the prebrachial i./c. (I), anterior ventral magnocellular (II, III), posterior part of the posterior lateral pedal (II), posterior pedal (II), and median basal (II) lobes (figure 3).

Bundle I contains both efferent and afferent fibres. They enter protrusions of the prebrachial lobe, laterally (interbrachial nerves 1, 2, 3) or ventrally (interbrachial nerve 4) to their relevant brachial nerve; these parts of the prebrachial lobe will be called "interbrachial lobules 1-4". There, the

efferents originate from 20 (lobule 1), or 40 (lobules 2-4 each) small and medium perikarya; these lie in all perikaryal layers (figure 27; see figure 15). The afferents of bundle I are mostly fine, but some are also medium. They cross the lobule and run, partly dividing dichotomously, in the corridor of the infrabrachial commissure (figure 22; see also figure 25). Some continue to the contralateral side.

Bundle II contains only fine afferent fibres. These reach the posterior part of the posterior lateral pedal lobe via two different pathways. The fibres of the interbrachial nerve 1 run dorsally through the suboesophageal mass, together with the afferent fibres of bundle III of the superior antorbital nerve. The fibres of the interbrachial nerves 2-4 run through the brachio-palliovisceral connective to leave it in dorsal direction at the level of the anterior ventral magnocellular lobe. There they join the corresponding bundle of the interbrachial nerve 1. The afferents of all four nerves spread in the neuropils of the anterior and posterior (behind the brachial-optic lobe tract) parts of the posterior lateral pedal lobe and in the neighbouring neuropils of the dorsal posterior pedal and anterior ventral magnocellular lobes (see figure 23). Some single fibres of at least the interbrachial nerves 2 and 3 run through the posterior basal-suboesophageal connective to end ventrally in the median basal lobe.

Bundle III contains afferent fibres. These are either large (5-15 μm) or very fine and run, together with ventral magnocellular fibres of the brachial nerves, through the brachio-palliovisceral connective to the anterior ventral magnocellular lobe (figure 26).

Bundle IV contains only efferent fibres. They originate from 130 large perikarya in the anterior pedal lobe: 45 perikarya of the interbrachial nerve 1 lie mainly dorsal and all 75 of the interbrachial nerves 2-4 mainly ventral. The interbrachial nerve 1 has about 10 additional large perikarya in the anteroventral part of the anterior lateral pedal lobe. The trunks of the neurons run, one per fibre channel, deep into the neuropil (see figures 17, 18, 20 and 21).

Bundle V occurs only in the interbrachial nerve 1 and contains efferent fibres. They originate from 35 medium perikarya that are situated mainly latero-posterior in the anterior chromatophore lobe (see figure 19). Their trunks may run together within a fibre channel into the neuropil. Fine varicose fibres run into the interchromatophore connective, but none were seen reaching the posterior chromatophore lobe; these fibres might be afferent.

(iv) *Head retractor nerves*

There are two head retractor nerves, an anterior and a posterior one. Both obviously contain only efferent fibres, i.e. no sensory information (such as from proprioceptors) runs through these nerves.

They leave the brain at the dorso-posterior margin of the suboesophageal mass. The anterior head retractor nerve runs laterally, the posterior one medially, at the sides of the posterior oculomotor nerve. In the brain, the fibres of both nerves mix in front of the posterior chromatophore lobe and continue as a single head retractor bundle to 650 medium and large perikarya in the anterior pedal, anteroventral part of the anterior lateral pedal, and posterior pedal lobes (figure 4).

The perikarya of the two nerves are equally distributed in these lobes. Posteriorly in the anterior pedal lobe, there are 50 perikarya each dorsally, and 70 perikarya each ventrally (about 300 μm behind the most anterior perikarya of the antorbital nerves). In the posterior pedal lobe, there are 100 - 150 perikarya each dorsally (anterior to the median basal to posterior pedal lobe tract), and about 80 perikarya each ventrally (anterior to the level of the anterior funnel lobe) (figures 28 and 29; figures 31, 32 and 34). Some perikarya cluster ventrally, around the entering median pallial retractor nerve. Posterior to the entry of the retractor nerve into the neuropil, the perikarya and their trunks and arborizations become restricted to the lateral parts of the posterior pedal lobe. Single additional perikarya were seen in the anteroventral part of the anterior lateral pedal lobe. In general, trunks of two or more neurons enter the neuropil together within one fibre channel. In the ventral anterior pedal lobe some of the collaterals are very long and reach to the anterior parts of the anterior pedal and anterior lateral pedal lobes. Presumptive extraocular motoneurons are obviously secondarily filled by head retractor neurons, with the site of contact being deep in the continuous anterior pedal/anterior lateral pedal neuropil (see figure 20).

(v) *Medial pallial retractor nerve*

The medial pallial retractor nerve enters the brain ventro-medially, immediately in front of the anterior funnel nerve. Its fibres run to the posterior edge of the middle pedal commissure, where they distribute. They are all efferent and originate from 230 medium and large perikarya in the anterior pedal, anteroventral part of the anterior lateral pedal, anterior lateral pedal, and posterior pedal lobes (figure 5).

There are 50 perikarya each ventrally, and 60 perikarya each dorsally, in the anterior and posterior pedal lobes. The perikarya are distributed in all perikaryal layers, the medium ones mainly antero-ventrally. Their distribution is similar to that of the perikarya of the head retractor nerves (figure 30; see also figures 28 and 34). Most posteriorly their distribution reaches the level of the posterior edge of the middle pedal commissure, most anteriorly it matches with that of the head retractor neurons. Additionally, some medium perikarya were seen in the inner perikaryal layers of the posteromedial part of the posterior pedal lobe, and the anteroventral anterior lateral pedal lobe.

(vi) *Anterior funnel nerve*

The number of bundles of the anterior funnel nerve is difficult to determine, but ten bundles (I-X) can be distinguished. Their efferents originate in the anterior chromatophore (VII), anterior funnel (I), anterior pedal (IX), posterior pedal (IX), anterior palliovisceral (IX), posterior ventral magnocellular (X) and median dorsal vasomotor (IV) lobes. Their afferents run to the anterior funnel (I), brachial (V, VI), anterior chromatophore (VII, VIII), anterior pedal (VI), posterior pedal i./c. (IV), anterior (II, III, IV i./c.), middle (II, III, IV i./c.) and posterior (III) ventral magnocellular, anterior and posterior palliovisceral (IV), posterior funnel (II), posterior chromatophore (VIII), median dorsal vasomotor (IV), lateral dorsal vasomotor (X), and lateral ventral vasomotor (X) lobes, and to the posterodorsal lobe (III) (figure 6).

Bundle I contains mostly efferent and a few afferent fibres. The efferents originate from 60 medium perikarya of all perikaryal layers of the anterior funnel lobe (figure 33; figure 37); there also the afferents terminate.

Bundle II contains fine and medium afferent fibres. Single, or several of these, run parallel in the ventral parts of the ventral magnocellular lobe in posterior direction. The bulk of these fibres is found in the anterior region of this lobe, but some proceed to its middle part (figure 35). They form several layers in the neuropil, at a distance of 70 to 450 µm from the lobe's ventral margin. Some fibres, or their collaterals, continue in transverse or vertical directions. The most lateral fibres, including the only ones that pass throughout the dorsoventral extent of the lobe, are about 300 µm away from the lobe's lateral margin. Posteriorly, the fibres end in front of the posterior magnocellular lobe. Single varicose fibres of bundle II terminate in the posterior funnel lobe. Some fibres can be followed into the incoming inferior ophthalmic nerve.

Bundle III contains very fine, fine and medium afferent fibres. These run parallel in posterior direction in the dorsal neuropil of all three parts of the ventral magnocellular lobe. They form several layers in the neuropil at a distance of 40 - 300 µm from its dorsal edge. The most lateral fibres run aside that fibre branch of the posterior root of the posterior superior ophthalmic nerve that passes to the palliovisceral, magnocellular and posterior pedal lobes. Some of these fibres can be followed deep into the neuropil beyond the anterior palliovisceral commissure. The most medial fibres are seen at the level of the medial margin of the posterior chromatophore lobe, whereas the most posterior fibres cross or join the pallial and collar nerves at their entry into the neuropil. Single fine varicose fibres of bundle III run dorsolaterally into the posterodorsal lobe (figure 35). In the dorsal part of the middle ventral magnocellular lobe, medium neurons are secondarily filled by some of these fibres.

Bundle IV contains afferent and efferent fibres. These run tangentially to the medial edge of the anterior funnel lobe and enter the palliovisceral and ventral posterior pedal lobes, directly lateral to the efferents of bundle IX. Its afferent fibres cross, mostly in bundles, the trunks of the neurons of the palliovisceral and anterior and posterior pedal lobes, mainly in their outer neuropil layers. The palliovisceral fibres of bundle IV are distributed in several layers of the anterior, and some in the posterior, palliovisceral neuropil. Some single afferent fibres reach to the median dorsal vasomotor lobe, others cross the fibres of the incoming posterior funnel nerve. In the median dorsal vasomotor lobe, single efferents also originate. The anterior and posterior pedal fibres of bundle IV are afferents and, as shown by double staining (see § 2), cross trunks of motoneurons of the medial pallial retractor nerve in the medial posterior part of the posterior pedal lobe, as well as anteriorly in its ventral and dorsal parts, at the level of the middle pedal commissure (which is the most anterior distribution of these afferents) (figure 30). Ipsi- and contralaterally, these pedal fibres also cross the fibres of the incoming medial pallial retractor and anterior funnel nerves. Some of the contralateral pedal fibres reach to the ventromedial neuropil of the contralateral anterior ventral magnocellular lobe.

Bundle V contains fine afferent varicose fibres. They enter the brachio-palliovisceral connective and run, as single fibres, in anterior direction. Some fibres were difficult to follow to their ends; some may end within the connective, whereas others, in the brachial lobe, were seen running a small distance into the fibre bundles of each of the four brachial nerves that enter the connective.

Bundle VI also contains fine afferent fibres. These run through the brachio-palliovisceral connective and enter, together with the inferior antorbital nerve, the neuropil of the anterior pedal lobe. The fibres reach into the ventral, and few into the dorsal, neuropil of the anterior pedal lobe; some continue forwards into the ventral, and few into the dorsal, neuropil of the brachial lobe.

Bundle VII contains both efferent and afferent fibres. They pass via the brachio-palliovisceral connective, and parallel to the bundle VI afferents through the anterior pedal neuropil, into the anterior chromatophore lobe. Some, probably afferent, fibres run for short distances within the anterior chromatophore commissure, but remain ipsilaterally. The efferents originate from 50 medium perikarya in the lateral parts of the anterior chromatophore lobe; there is some uncertainty whether all these neurons belong to bundle VII efferent fibres.

Bundle VIII probably contains only afferent fibres. It runs through the ventral magnocellular and palliovisceral lobes to the posterior chromatophore lobe. Most afferent fibres are medium and varicose and run to the anterior chromatophore lobe via the interchromatophore connective (figure 35). In both the anterior and posterior chromatophore lobes, they end in various depths of mainly the outer neuropil layers. A few fibres are perhaps efferent, but their perikarya have not been seen.

Bundle IX contains only efferent fibres. It might be further subdivided into a pedal and a palliovisceral bundle. The fibres originate from 230 (anterior pedal) and 1,750 small, medium and large perikarya in the anterior and posterior pedal and the anterior palliovisceral lobes. Almost all perikarya of the pedal lobes are concentrated medially, with the exception of some laterally to the entry of the anterior funnel nerve into the neuropil of the ventral posterior pedal lobe. This contrasts with the perikarya of the palliovisceral lobe, which are distributed all over the surface of the lobe. In the ventral anterior pedal lobe the most anterior perikarya are found at the level of the anterior edge of the middle pedal commissure. In the dorsal anterior pedal lobe they lie about 300 μm further anterior. Their trunks enter the neuropil one per fibre channel. In the posterior pedal lobe the medium and large perikarya are distributed more evenly and several trunks may enter a single fibre channel. In the palliovisceral lobe the efferents originate from 300 medium and large perikarya: 80 perikarya anteromedially, 70 ventrally and 150 perikarya dorsally. Dorsally, the most posterior perikarya lie anterior to the continuous posterior chromatophore and palliovisceral neuropil, ventrally they lie anterior to the posterior funnel lobe. The trunks of the neurons enter the neuropil one per fibre channel (figures 33 and 37; see figures 36 and 40).

Bundle X contains efferent and afferent fibres. The efferents run to the centre of the posterior suboesophageal mass and divide into dorsal and ventral directions. Dorsally, they originate from 30 large perikarya in the medial part of the posterior ventral magnocellular lobe (anteriorly and medially to the dorsolateral vasomotor lobe); ventrally they originate from 10 large perikarya between the ventrolateral and the ventromedial vasomotor lobes (figure 41). Single medium, extremely varicose afferent fibres enter the lateral ventral and lateral dorsal vasomotor lobes. They run parallel to trunks of vasomotor neurons and end in inner perikaryal layers of the lobes.

(vii) *Posterior funnel nerve*

The posterior funnel nerve enters the neuropil together with the visceral nerve, anterior to the lateral ventral vasomotor lobe at the posterolateral edge of the palliovisceral lobe. At its entry, it divides into six bundles. Their efferents originate from the posterior funnel (I) and anterior palliovisceral (VI) lobes. Their afferents run to the posterior pedal i./c. (IV), anterior palliovisceral i./c. (IV, V), posterior funnel (I), anterior (II), middle (II) and posterior (III) ventral magnocellular (II,III), and lateral ventral vasomotor (III?), and posterodorsal lobes (III) (figure 7). Thus, compared with the anterior funnel nerve, the organization of the posterior funnel within the central nervous system is less complex (e.g. no connections with the brachial, anterior pedal and chromatophore lobes; compare figures 6 and 7).

Bundle I contains both efferent and afferent fibres. The efferents originate from 60 small and

medium perikarya in all perikaryal layers of the posterior funnel lobe (figure 38). The afferents cross the trunks of the efferents at varying angles; this is different from most other lobes where the afferents cross the trunks of the efferents at right angles (see § 3.a)

Bundle II contains only afferent fibres. They are very fine and run as single fibres in longitudinal direction to the posterior end of the brachio-palliovisceral connective; there they terminate in the anterior (few) and middle ventral magnocellular lobes (figure 38).

Bundle III is small and contains only very fine afferent fibres. They run into the posterior ventral magnocellular lobe within the pathway that connects the posterior funnel nerve with the pallial and collar nerves as well as into the magnocellular root of the posterior superior ophthalmic nerve. Some fibres can be seen running to in these nerves at their entry into the palliovisceral neuropil. Others run to the posterodorsal lobe. Single, extremely varicose fibres, which cannot be related to this bundle with certainty, terminate in the neuropil of the lateral ventral vasomotor lobe.

Bundle IV also contains very fine afferent fibres. These enter the palliovisceral lobe lateroventrally to proceed for about 200 μm, in anterior direction. Further very fine afferent fibres run deep into the anterior palliovisceral neuropil and from there in anterior direction to the continuous palliovisceral/posterior pedal neuropil. Some varicose fibres reach to the posterior pedal lobe; there, some cross palliovisceral efferent fibres of bundle IX of the anterior funnel nerve (figures 43 and 44).

Bundle V contains afferent fibres. They spread from the centre of the palliovisceral lobe to run nerve. The afferents run close together and are restricted to those parts of the anterior palliovisceral lobe where the bundle VI efferent trunks occur (figures 36, 40, 43 and 44).

There are many single, very fine and mostly varicose fibres, which cannot be related to bundle V with certainty; they may also belong to bundles III or IV. These fibres distribute throughout the medial neuropil of the ipsi- and contralateral palliovisceral lobes. There, the most posterior fibres are seen in the ventral parts of the posterior palliovisceral lobe, anterior to the median ventral vasomotor lobe and mainly beneath the bundle VI efferents of the visceral nerves. Some contralateral afferent fibres spread in the medial neuropil of the anterior palliovisceral lobe, anterior and lateral to the lateral vasomotor tract. Contralaterally, single fibres reach to the posterior pedal lobe at the level where its medial neuropil is continuous with that of the palliovisceral lobe.

Bundle VI contains only efferent fibres. They originate from 320 mainly large and some medium perikarya in the anterior palliovisceral lobe: 200 frontomedially, 70 ventrally, and 50 dorsally.

Their distribution coincides with that of the palliovisceral efferents of bundle IX of the anterior funnel nerve (figures 40 and 43). The neurons enter the neuropil one or several per fibre channel. Some secondarily filled efferents have also been observed (figure 36).

(viii) *Collar nerve*

The collar nerve enters the brain together with and dorsolateral to the pallial nerve. At its entry, it divides into four bundles. Their efferents originate from the posterodorsal lobe (I), the lateral dorsal vasomotor (III), posterior chromatophore (II), and anterior and posterior palliovisceral (III) lobes. Their afferents run to the posterior funnel (IV), posterodorsal (I), anterior and middle ventral magnocellular (IV) and anterior and posterior palliovisceral (IV) lobes and into the extracortical neuropil (IV) (figure 8).

Bundle I contains efferent fibres that run dorsolaterally in the nerve. They originate from numerous small and some medium perikarya in all perikaryal layers of the posterodorsal lobe (figure 39). Bundle I may also contain a few afferent fibres.

Bundle II also contains efferent fibres. They originate from medium perikarya of all perikaryal layers of the posterior chromatophore lobe.

Bundle III is large and again contains only efferent fibres. They originate from 600 medium and large perikarya in the anterior and posterior palliovisceral lobes: 140 perikarya frontomedially, 100 perikarya dorsally and posterior to the neuropil connection between the posterior chromatophore and palliovisceral lobes (mainly in its medial and lateral parts), 300 perikarya dorsally and anterior to the neuropil connection between the posterior chromatophore and palliovisceral lobes (nearly all in its medial and posterolateral parts), and 60 perikarya ventrally in its lateral and medial parts, with the most posterior perikarya anterior to the medial edge of the posterior funnel lobe (figure 42). A few efferents have been stained in the dorsolateral vasomotor lobe; they may either belong to bundle III or to an additional bundle V.

Bundle IV contains afferent fibres. They terminate in the anterior and posterior palliovisceral and anterior and middle ventral magnocellular lobes. In the posterior aspects of the anterior palliovisceral lobe very fine, fine and medium afferents cross, deeply in the neuropil, some efferents of bundle III, or join or cross fibres of the posterior funnel nerve. Single fibres reach to the anterior palliovisceral neuropil at the level where it is continuous with that of the posterior pedal lobe. In the ventral parts of the palliovisceral lobe, some medium afferents pass underneath the posterior funnel lobe and run to the extracortical neuropil (see figures 48 and 49); very small output neurons of the visceral nerve also originate there. Single fine fibres terminate in the

posterior funnel lobe (figure 48). In the ventral neuropil of the anterior ventral magnocellular lobe some medium afferents spread from anterior to posterior.

(ix) *Visceral nerve*

The visceral nerve enters the brain at its ventrocaudal margin. At its entry it divides into six bundles. Their efferents originate from the median ventral vasomotor i./c. (II, III), median dorsal vasomotor i./c. (I), lateral ventral vasomotor (II), lateral dorsal vasomotor (I), posterior ventral magnocellular i./c. (III), and anterior and posterior palliovisceral (VI) lobes, as well as from perikaryal layers of the posterior ventrolateral suboesophageal mass that surround an extracortical neuropil (IV, V). Their afferents run to the median ventral vasomotor i./c. (II, III), median dorsal vasomotor i./c. (I), lateral ventral vasomotor i./c. (VI), posterior funnel i./c. (VI), posterior ventral magnocellular i./c. (VI), and the anterior i./c. and posterior palliovisceral (VI) lobes, as well as to the posterodorsal lobe (VI) (figure 9).

Bundle I contains efferent fibres. They diverge posterolaterally from the nerve and pass outside the ventrolateral perikaryal layers of the brain to enter the median dorsal vasomotor lobe. Before reaching the neuropil, the bundle separates into two branches. These originate from 1900 very small, small and medium perikarya which are distributed in all, but mainly the outer perikaryal layers of the ipsi- and contralateral median dorsal vasomotor lobes. There, trunks of several neurons run within one fibre channel. Sometimes, single medium, extremely varicose fibres terminate in the neuropil that protrudes into the perikaryal layers; these fibres might be afferent. A few small perikarya were seen in the perikaryal layers of the lateral dorsal vasomotor lobe (figure 45).

Bundles II and III both contain efferent fibres. They enter the median ventral vasomotor lobe posterolaterally (bundle II) and anteromedially (bundle III), respectively. They originate from 1900 very small, small and medium perikarya of the ipsi- and contralateral lobes (figure 45). Sometimes single medium, extremely varicose fibres terminate in the neuropil that protrudes into the perikaryal layers; these fibres might be afferent. Some of the bundle II and III perikarya lie ventrally in the ipsi- and contralateral posterior ventral magnocellular lobes between the ventral vasomotor and posterior funnel lobes (figure 46). A few small perikarya, with fibres of probably bundle II origin, were seen in the perikaryal layers of the lateral ventral vasomotor lobe.

Bundles IV and V contain only efferent fibres. They separate laterally from the visceral nerve to originate from small and very small perikarya in the ventrolateral margin of the suboesophageal mass; however, their trunks and fibres do not enter the vasomotor lobe but join the extracortical neuropil (see Young 1971) (figure 49).

Bundle VI contains both afferent and efferent fibres. It may be further subdivided into bundles that pass to various suboesophageal parts of the brain. The efferents originate from 900 small (few), medium and large perikarya of the anterior and posterior palliovisceral lobes. Their area of distribution matches that of the collar nerve (see § 3.c.viii); in the dorsal part of the palliovisceral lobe, the most numerous perikarya lie medially and posterolaterally. One or two trunks of the efferents may enter the neuropil in a single fibre channel. Their collaterals form layers of fibres in different depths of the neuropil. Some of these collaterals reach to the neuropil of the posterior funnel and the contralateral median palliovisceral lobes (figures 46 and 47; see also figure 42). Single fine and medium afferent fibres cross the trunks of the efferent neurons; some can be traced to the posterior pedal and others to the contralateral anterior palliovisceral lobe. Single medium afferent fibres leave bundle VI and pass to the posterior ventral magnocellular lobe. Some fibres cross in the corridor of the posterior palliovisceral commissure to the contralateral side. Other afferents were seen in the ipsi- and contralateral posterior ventral magnocellular lobes. At the level of the posterior chromatophore commissure, bands of 20-30 parallel fibres, including very fine ones, separate from bundle VI. They run to the posterodorsal lobe, to the ipsi- and contralateral posterior funnel lobes, to the posterior ventral magnocellular lobe around the incoming pallial and collar nerves, to the lateral dorsal and some to the ipsi- and contralateral lateral ventral vasomotor lobes (figure 46).

(x) *Brachial, pallial, extraocular eye muscle and statocyst nerves*

Using cobalt and/or HRP tracer techniques, the course and distribution of efferent and afferent fibres have already been described in detail for the brachial, pallial, extraocular eye muscle and statocyst nerves (Colmers 1982; Budelmann & Young 1984, 1985; Saidel & Monsell 1986). Their results for the most part were confirmed in this study and will not be described again in this paper. Instead, wherever careful revision of their material and new fillings gave different results, these will be described here. Previous and new results are summarized diagrammatically in figures 10-13.

Moreover, to meet the aim of this paper, for some lobes the location of the efferent perikarya and the termination of the afferent fibres will be described in more detail with respect to the subdivisions of the lobes.

Brachial nerves (figure 10). Centripetal filling of the fourth brachial nerve resulted in no further afferent and efferent supraoesophageal pathways than described for the third brachial nerve (Budelmann & Young 1985). However, for both nerves perikarya were seen in two more suboesophageal lobes: anteroventrally in the anterior lateral pedal lobe (single perikarya; figure 52) and anteromedially in the contralateral anterior pedal lobe. In the ipsilateral anterior pedal lobe, the

bulk of perikarya of the fourth brachial nerve lies medially to that of the third brachial nerve (figures 50 and 51). The perikarya in the posterior ventral magnocellular i./c. lobes were found dorsally between the median and lateral dorsal, and ventrally between the median and lateral ventral vasomotor lobes (these are the regions, where the bundle X efferent fibres of the anterior funnel nerve originate).

Afferent fibres of the brachial nerves could be followed into six more suboesophageal lobes: into the anterior part of the contralateral anterior pedal lobe, the ipsi- and contralateral posterior pedal and the posterior part of the posterior lateral pedal lobes, the anterior and posterior funnel lobes and the posterodorsal lobe. In the brachial lobes, some single afferent fibres were seen terminating in the interbrachial lobules. In all three parts of the ventral magnocellular lobe, the afferent fibres were abundant on both sides and some fibres were found in the posterior palliovisceral lobe. Single fibres enter the median optic-ventral magnocellular lobe tract.

So far, no obvious differences have been observed between fillings of the third and fourth brachial nerves; but further fillings are necessary to admit no doubt that this is a general rule for all brachial nerves, including the first.

Pallial nerve (figure 11). Contrary to Saidel & Monsell (1986), no perikarya were seen in the superior buccal and the lateral dorsal and lateral ventral vasomotor lobes. Single perikarya were seen anteroventrally in the anterior lateral pedal lobe (figures 52-54); others were seen ventrally in the anterior pedal lobe around the incoming medial pallial retractor nerve. The perikarya in the ventral magnocellular lobe were seen ventrally in its middle part and ventrally and caudally in its posterior parts on both sides. Perikarya were found dorsally between the median and lateral dorsal, and ventrally between the median and lateral ventral vasomotor lobes (these are the regions, where also efferents/motoneurons of the brachial nerve and of bundle X of the anterior funnel nerve originate).

Afferent fibres of the pallial nerve could be followed into eight more lobes: the anterior pedal lobe (except its antero-dorsal part), the anterior and posterior lateral pedal lobes, the posterior pedal lobe, the ipsi- and contralateral anterior, middle and posterior ventral magnocellular lobe, the anterior i./c. and posterior i./c. funnel lobes and the posterodorsal i./c. lobes. Single fibres enter the medial ventral magnocellular to optic lobe tract. The afferent fibres running into the brachial lobe could be followed to the lateral parts of the posterior prebrachial lobe.

Extraocular eye muscle nerves (figure 12). For the two eye muscle nerves that carry ganglia, the inferior ophthalmic nerve and the posterior root of the posterior superior ophthalmic nerve, perikarya were found in three more lobes: in the posterior pedal lobe, in the middle ventral

magnocellular lobe dorsally (few medium perikarya), and in the anterior palliovisceral lobe. The efferents originate from perikarya in four regions: (i) Some medium and large perikarya in the dorsal anterior palliovisceral lobe. (ii) Large perikarya at the level of, and anterior to, the ventral branch of the posterior superior ophthalmic nerve (figure 57); the most anterior ones lie immediately behind the most posterior perikarya of the head retractor nerves in the posterior pedal lobe. (iii) Perikarya in the anteroventral anterior palliovisceral lobe, immediately posterior to the ventral posterior pedal perikarya of these nerves. (iv) Medium perikarya in the medial anterior palliovisceral lobe (only for the posterior root of the posterior superior ophthalmic nerve). In addition, small perikarya of the inferior ophthalmic nerve are located in the lateral anterior ventral magnocellular lobe.

Centripetal cobalt filling of two branches of the anterior oculomotor nerve, innervating muscles of antagonistic function (the anterior inferior oblique and minor anterior rectus muscles; Budelmann & Young 1984), showed an overlapping distribution of perikarya in the anterior lateral pedal lobe. The perikarya were restricted to a region anterior to the anterior basal-pedal lobe tract. Centripetal cobalt filling of the branch of the middle superior ophthalmic nerve that innervates the superior rectus muscle showed the same pattern of distribution of perikarya as does the whole nerve, and thus indicate the absence of a somatotopy.

Afferent fibres of the inferior ophthalmic and posterior root of the posterior superior ophthalmic nerves could be followed into six more lobes: (i) the posterior ventral magnocellular lobe, at the level of the middle and posterior palliovisceral commissures, with some fibres running from the ipsi- to the contralateral side; (ii) the dorsolateral posterior and anterior palliovisceral lobes, as bundles of very fine fibres close to the perikaryal layers; (iii) the anterior and (iv) the posterior funnel lobes (both only for the inferior ophthalmic nerve); (v) the inner neuropil layers of the posterior parts of the ipsi- and, via the contralateral median basal lobe, contralateral posterior lateral pedal lobes; and (vi) the posterior parts of the anterior pedal lobe, laterodorsally (only posterior root of the posterior superior ophthalmic nerve) and ventrally.

Retrograde filling of the anterior oculomotor nerve resulted in some stained afferent fibres in the macula and crista nerves, secondarily filled in the anterior lateral pedal lobe. After double intensification these fibres could be traced to their perikarya in the macula and crista, respectively (figure 58).

Statocyst nerves (figure 13). Perikarya of macula and crista efferents were seen dorsally and ventrally in the lateral parts of the anterior palliovisceral lobe and posterolaterally in the posterior pedal lobes. A cluster of perikarya in the anterior lateral pedal lobe was seen anteroventrally. Some perikarya of all statocyst nerves lie in a lobule anteroventrally in the anterior and posterior part of

the posterior lateral pedal lobe, at the entry of the nerves (figure 59).

Macula and crista afferents could be followed into three more lobes: (i) the ipsilateral, and also lateral parts of the contralateral, anterior pedal lobes; (ii) the ipsilateral (new for crista fibres, figure 56) and contralateral posterior pedal lobes; the contralateral distribution of (i) and (ii) fibres are different for the macula and crista nerves; and (iii) the ventral brachial lobe (it is still unclear whether macula afferents project there). In the anterior palliovisceral lobe, macula afferents were found medially. Macula and crista afferents run through the centre of the middle ventral magnocellular lobe to terminate in the posterior ventral magnocellular lobe at the level of the middle and posterior palliovisceral commissures (figure 55).

4. DISCUSSION

In the following discussion, special emphasis is paid to general aspects of functional organization of the *Octopus* sensory-motor lobes, rather than to discuss the significance of single fibre pathways. The large body of information now available for the *Octopus* brain allows comparison of its motor organization with that of vertebrates and insects (see also discussions in Plän 1987; Plän & Budelmann - a & b, in preparation). Although most of the previous stimulation experiments in cephalopods were done with *Sepia* (Boycott 1961; equivalent work on *Octopus* remained unpublished) their basic results apply, with little modification, to *Octopus* as well (see Wells 1978) and thus have been used when discussing the neuroanatomical findings.

(a) *Motor organization of the suboesophageal lobes of* Octopus

(i) *Differences in the motor organization of vertebrates, insects and* Octopus

Topographical orders in the pattern of neuronal organization generally represent the function and/or spatial location of receptors and effectors. The most obvious topographical order is the somatotopic one, where the peripheral location of sensory and motor units is reflected in the position of afferent and efferent units in the central nervous system.

In vertebrates, there is a clear somatotopic representation. Motoneurons of distinct nerves, as well as of distinct branches of these nerves, form motoneuron pools, e.g. in distinct regions of the ventral horn of the spinal cord and the cranial nerve nuclei in the brainstem; only occasionally do the pools show some overlap. The position of a motoneuron pool moreover reflects the location of its effectors; for instance, lateral motoneuron pools in the cervical and lumbosacral enlargements of the spinal cord innervate distal (girdle or limb) muscles and medial neurons proximal (axial) muscles. This somatotopy also correlates with function: there are different motoneuron pools for

functionally antagonistic or synergistic muscles of the same skeletal part, for example, flexors and extensors, or red and white muscles (see Kuypers 1982; Kelly 1985; Mos & Williamson 1986; Withington-Wray *et al.* 1986; Ghez 1991).

In insects, there is only little somatotopic representation of the innervated muscles. The location of a motoneuron perikaryon within the suboesophageal or a thoracic ganglion is a rough projection of the muscle it innervates. Perikarya whose axons exit through the same nerve root are grouped together, and perikarya of motoneurons that drive the same muscle are adjacent (see Bentley 1970; Honegger *et al.* 1984). This somatotopy, however, does not correlate with function (see also Burrows 1996). The wing, leg or mouthpart motoneurons for motor patterns such as flight, walking and feeding, respectively, lie together but innervate muscles which may be spaced distantly from each other. The neurons for one function may originate from different sites of one or even two ganglia. To ensure coordination of the motoneurons participating in one of these motor patterns, a different method from that of vertebrates has evolved: the arborizations of the motoneurons widely overlap and form meshworks. This overlap is of functional significance, because the synaptic interaction in invertebrate brains is mainly found in the neuropil and not in the gray perikaryal matter as in vertebrates (see Bullock & Horridge 1965).The motoneuron meshworks also integrate motoneurons of both synergistic and antagonistic function, for example, wing depressors and elevators. Motoneuron meshworks innervating different effector systems (neck and mouthparts, legs and wings), at best slightly overlap (Altman, 1981; Honegger *et al.* 1984; Altman & Kien 1985).

In *Octopus*, contrary to vertebrates and insects, there is no somatotopic arrangement. Although the neurons of the different effector systems originate in different brain regions (see § 4.a.ii), the efferents of a single effector system, e.g. the motoneurons of the different extraocular or funnel muscles, show no somatotopic arrangement but are equally scattered in the relevant brain region. The location of motoneurons does not represent the position of the innervated muscles, for example, the motoneurons of the anterior and posterior oculomotor nerves, which innervate widely separate extraocular muscles, originate mixed together throughout the anterior lateral pedal lobe (Budelmann & Young 1984). Again chromatophore motoneurons of the pallial nerve that innervate neighbouring skin areas of the mantle originate from all parts of the posterior chromatophore lobe (Dubas *et al.* 1986). Also, the motoneurons are not grouped according to their function, e.g. motoneurons of nerves that innervate antagonistic muscles originate from the same regions of the relevant suboesophageal lobes (Budelmann & Young 1984; Plän, unpublished).

These neuroanatomical findings confirm earlier physiological experiments in *Sepia* and *Octopus* (Boycott 1961; see also Wells 1978): stimulation of any part of the prebrachial, brachial, anterior pedal, posterior pedal, anterior lateral pedal or palliovisceral lobes elicits the same lobe-specific

motor reactions and thus indicates that the relevant motoneurons are distributed throughout the lobes. The same is true for peripheral ganglia; there, stimulation of different parts of the stellate or arm ganglia always results in overall movements of the innervated muscles (Wilson 1960; Rowell 1963). In a few *Octopus* lobes (brachial, anterior and posterior pedal, and anterior lateral pedal), efferent/motoneuron meshworks occur as in insects, with arborizations of neurons that overlap widely. These neurons drive motor reactions of only one effector system. In most *Octopus* lobes, however, overlap occurs between motoneurons of different effector systems, for example, arms and head, head and funnel, and funnel and mantle (see § 4.a.ii). Probably due to this overlap, electrical stimulation results in overall reactions of several effector systems (Boycott 1961).

Thus, different principles of motor organization have evolved in these three animal groups. The different degrees of topographical order at the motoneuron level require different integrative synaptic mechanisms for picking out the appropriate motoneurons for the execution of a motor behaviour. In vertebrates, the final motor output for a behaviour that includes just a single effector system will be achieved by the coordinated activation of motoneurons in different motoneuron pools. In insects, the activation alternates between functionally different motoneurons of the same motoneuron meshwork. The same is true in *Octopus*; however there, in addition, the motoneurons of the other effector system in the meshwork have to be kept free of activation. Conversely, if a motor behaviour is to be executed that includes two effector systems simultaneously, then in vertebrates and insects motoneurons in several pools or meshworks have to be activated at the same time; in *Octopus*, however, it might be sufficient to coactivate motoneurons of a single motoneuron meshwork.

(ii) *Motoneuron composition of* Octopus *suboesophageal lobes*

In *Octopus*, the perikarya and arborizations of the motoneurons (and further efferents/motoneurons) of the nerves originate from extended but discrete suboesophageal brain regions. These regions match well for those nerves that belong to the same effector system, for example, for the seven eye muscle and for the two funnel nerves. As is shown in figures 60-62, regions of some nerves of different effector systems overlap partly, widely or even totally. In the prebrachial, brachial and anterior pedal lobes, the arm efferents/motoneurons form the area 1. This area overlaps in the anterior pedal lobe with those of the head (area 2) and pallial (area 6) motoneurons. In the anteroventral part of the anterior lateral pedal lobe, all three areas (1, 2, and 6) overlap slightly with the area of the extraocular motoneurons (area 3; see below). In the palliovisceral and ventral magnocellular lobes, the areas of the funnel and mantle (areas 5 and 6), brachial (area 1), and ophthalmic motoneurons (area 4) and the statocyst efferents (area 7) overlap. (The ophthalmic motoneurons of area 4 are not oculomotor neurons but those of the inferior ophthalmic and posterior superior ophthalmic nerves that originate outside the anterior lateral pedal lobe). The area

of the statocyst efferents (area 7) also overlaps with the area of the extraocular motoneurons (area 3).

There are three regions where efferents/motoneurons of only one effector system occur: (i) the prebrachial, brachial and frontal anterior pedal lobes with efferents/motoneurons of the arms, (ii) the anterior lateral pedal lobe, with the exception of its anteroventral part (figure 60), with motoneurons of the extraocular eye muscles, and (iii) the posteromedial posterior pedal lobe with motoneurons that innervate distinct muscles of the funnel tube (Plän, unpublished). In *Octopus*, these three effector organs have a highly complex muscle system and their control surely requires an elaborate coordination of their motoneurons. This coordination might be further complicated by the interaction with motoneurons of other effector systems.

The distribution of the efferents/motoneurons within the various suboesophageal lobes is summarized diagrammatically in figures 63-67. It allows subdivision of each lobe into a varying number of subregions. With the exception of the anterior dorsal and ventrolateral prebrachial lobes, in all subregions the arborizations of the efferents/motoneurons overlap widely and thus form rather regular "dendritic" meshworks; from electron microscopical work, there is evidence of mutual synaptic interactions between these overlapping neurons, i.e. "dendrites" may be pre- or postsynaptic (Plän 1983). Arborizations of interneurons are also integrated in these meshworks (Plän & Budelmann - a & b, in preparation).

The overlap of neurons probably provides the base for the coactivation of neurons of different nerves of the same and/or different effector systems (see Plän & Budelmann - a & b, in preparation). A coactivation of neurons of different effector systems may also occur for motoneurons of the arms, eyes and funnel tube. Despite their separate location, these motoneurons show an overlap with motoneurons of other nerves (i.e. other muscle systems) in other subregions of the anterior (brachial nerves), posterior (funnel nerves), and anterior lateral pedal lobes (eye muscle nerves).

By far the most dense area of overlap of efferents lies in the anteroventral part of the anterior lateral pedal lobe, including the area above the brachio-palliovisceral connective (figure 60). There, efferents of the antorbital, first interbrachial, brachial, head retractor, medial pallial retractor, pallial, the seven eye muscles, and the macula and crista nerves originate; also interneurons that project to other lobes cluster there (Plän & Budelmann - a & b, in preparation). This accumulation of neurons provides an overlap of the eye muscle motoneurons with motoneurons of all the other muscle systems. The motoneurons, in turn, all show mutual overlap. This overlap provides the possibility for coactivation of efferents of different nerves (see § 4.a).

Saidel and Monsell (1986) have stained neurons in the anteroventral part of the anterior lateral pedal lobe by centripetal filling of the pallial nerve with HRP. They considered them to be chromatophore motoneurons outside the anterior chromatophore lobe, because their axons run together with the anterior chromatophore bundle of this nerve. This running together has also been observed in the present cobalt findings. Nonetheless, these neurons and those of the other nerves in this subregion most probably are not chromatophore in nature, since the axons of the antorbital, interbrachial and brachial neurons in the anteroventral anterior lateral pedal lobe clearly enter the pedal, and not the chromatophore, bundles of these nerves; for the pallial nerve, however, the chromatophore bundle is the only way to reach the anterior parts of the brain.

It still remains unclear whether the ophthalmic neurons (area 4) in the posterior pedal, palliovisceral and ventral magnocellular lobes play a role in the control of eye movements. Electrical stimulation of these lobes never resulted in eye movements (Boycott 1961). On the other hand, threshold stimulation of the posterior superior (posterior root) and inferior ophthalmic nerves elicits coordinated movements of the eyes and head mediated by the extraorbital and nuchal muscles (Plän, unpublished), in addition to pupil movements and to eye movements mediated by the extraocular muscles (Budelmann & Young 1984). Possibly, the relevant motoneurons are (part of) those of area 4 that lie in the same or adjacent regions as do the head motoneurons. Whether some of the ophthalmic motoneurons of either area 4 or area 3 control the narrowing of the pupil also remains unclear. There are hints for the latter area, because the relevant motoneurons of the medial superior ophthalmic nerve, whose stimulation yields dilation of the pupil, originate in the anterior lateral pedal lobe only (Budelmann & Young 1984).

(iii) *Lower and intermediate motor centres - problems of definition*

The brachial ganglia, the stellate ganglion and the chromatophore lobes have been called lower motor centres, i.e. stimulation of lower motor centres produces only local reactions (Sanders & Young 1940; Boycott 1961; Young 1971; Wells 1978); this might point to a somatotopic relationship between motoneurons and their effectors. Such a somatotopic relationship, however, has not been found in the present study of the *Octopus* prebrachial, brachial, pedal, palliovisceral, chromatophore and lateral vasomotor lobes. An absence of a somatotopic organization is also obvious by the findings that there are no distinct motoneuron pools of the different stellar nerves within the stellate ganglion, of the different nerves of the brachial ganglia within each brachial ganglion, and of the chromatophore fibres of the pallial nerve within the posterior chromatophore lobe (Wilson 1960; Rowell 1963; Monsell 1980; Dubas *et al.* 1986). On the other hand, a somatotopic organization, according to the definition of a lower motor centre (see references above), occurs at various more peripheral levels: (i) the stellar nerves of the stellate ganglion innervate adjacent fields of mantle and skin muscles and mantle chromatophores (Wilson 1960;

Bühler *et al.* 1975; Ferguson *et al.* 1988); (ii) the nerves of the brachial ganglia serve discrete areas of arm and skin muscles (Rowell 1963); (iii) the head and funnel nerves innervate neighbouring areas of the head and funnel muscles (Pfefferkorn 1915; Plän, unpublished); (iv) the chromatophore fibres of different nerves innervate neighbouring body parts (Froesch 1973); and (v) the eye motor nerves innervate different eye muscles or (in case of the overlapping innervation) neighbouring parts of the same eye muscle (Budelmann & Young 1984). It is still unclear, however, whether there is a somatotopic arrangement of the different efferents of the visceral nerve within the median vasomotor lobes, of the funnel nerves within the funnel lobes, of the collar nerve within the dorsolateral lobe, of the interbrachial nerves within the interbrachial lobules, and of the different peripheral nerve fibres of the arms within the brachial nerve cords. In case there is, then these lobes and ganglia may fit into the definition of a lower motor centre.

In summary, all these data indicate how difficult, or even impossible, it is to correctly apply the terms "lower" and "intermediate motor centres" to cephalopod brains. Furthermore, anatomical and physiological definitions do not correspond and, therefore, different authors have characterized the same lobes differently (Sanders & Young 1940; Boycott 1961; Young 1971; Wells 1978). Also, the stimulation upon which the functional definitions of lower and intermediate motor centres are based (Boycott 1961) were done in isolated suboesophageal brain preparations only. Therefore, as long as there is a considerable lack of physiological data (for example, concerning the role of the interneurons in the suboesophageal lobes or the interaction of sub- and supraoesophageal parts of the brain) it is certainly too early to try a precise redefinition of the motor parts of the brain; it may even be impossible because the definitions will vary depending upon the effector system described (the same brain region that is lower in one effector system might be intermediate in another). Consequently, if in the meantime the use of the terms "intermediate" and "lower motor centres" is deemed unavoidable, they should at least be handled with more care than in many of the previous publications.

(b) ***Sensory organization in the suboesophageal lobes of*** **Octopus**

(i) *Sensory projections*

The afferent inputs to the sub- and supraoesophageal motor lobes enter the respective neuropil meshworks, cross many fibre channels and finally run parallel to collaterals of moto- and interneurons. There, many input fibres make synapses (some are "en passant" synapses; Plän 1983) with collaterals and/or trunks of the motoneurons and other efferents (Plän 1983). The input fibres run either into motor output regions or they converge into five subregions (A-E) of the suboesophageal brain (figures 60-62). The subregions A and B are unilateral. The subregions C-E, in contrast, have fibres crossing to the contralateral side. All five subregions, different from the rest

of the suboesophageal brain, get input from the optic lobes as well (Plän & Budelmann - a & b, in preparation).

Subregion A (figure 60). This is the posterior part of the posterior lateral pedal lobe and the confluent ventroanterior median basal lobe (including parts of the ventral precommissural and lateral posterior pedal lobes). The subregion A gets input from the statocyst nerves, the posterior superior ophthalmic (posterior root) and inferior ophthalmic nerves, the pallial nerve, the brachial nerves, the antorbital nerves, and the interbrachial nerves; at least at the level of the ventroanterior median basal lobe, the inputs come from the contralateral side as well.

Subregion B (figures 60 and 61). This is the middle and the anterior ventral magnocellular lobe. Subregion B gets ipsilateral input from the same sources as subregion A and further inputs from the anterior funnel nerve, the posterior funnel nerve and the collar nerve; the inputs from the brachial, pallial and anterior funnel nerves come from the ipsi- and the contralateral side. Since the ventral magnocellular lobe is connected with all sensory-motor lobes, it may perhaps have a modulating role and be involved in a system of activation and arousal (Plän & Budelmann - a & b, in preparation).

Subregions A and B are characterized by few (B) or none (A) motoneuron outputs; conversely, the statocyst efferents originates there. The two subregions act together in suboesophageal motor control. Subregions A and B are the only suboesophageal regions that get inputs from both the optic and the peduncle lobes (Plän & Budelmann - a & b, in preparation).

Subregion C (figures 60-62). This is the posterior ventral magnocellular lobe. Subregion C gets input from the ipsi- and contralateral statocyst, posterior superior (posterior root) and inferior ophthalmic, anterior funnel, brachial, pallial and visceral nerves. Efferents of the visceral nerve of presumed vasomotor character originate in this subregion. Perhaps subregion B and C together are involved in a system of activation and arousal, with the posterior ventral magnocellular lobe controlling inner organs (see Plän & Budelmann - a & b, in preparation, for discussion).

Subregion D (figures 61 and 62). This is the central brachial lobe. Subregion D gets input from the ipsi- and contralateral antorbital, anterior funnel, mantle, brachial and interbrachial nerves. In addition, ipsi- and contralateral input fibres of numerous sensory-motor lobes converge here. This lobe may possibly play the main role in the left-right-coordination of the arms (Budelmann & Young 1985; Plän & Budelmann - a & b, in preparation).

Subregion E (figures 60-62). This subregion lies at the level of the infrabrachial commissure. Like subregion D, it gets input from the ipsi- and contralateral antorbital, brachial and interbrachial

nerves. Some of the input fibres that run parallel to the infrabrachial commissure end around the roots of the brachial nerves, together with fibres of the statocyst, pallial and anterior funnel nerves, and fibres of the optic and ventral magnocellular lobes (Budelmann & Young 1985; Plän & Budelmann - a & b, in preparation). The function of this convergence is unclear.

Further afferent inputs run to motor output regions. They can be classified into (i) funnel and collar afferents, (ii) brachial, pallial and statocyst afferents, and (iii) afferents of the posterior superior ophthalmic (posterior root) and inferior ophthalmic nerves.

Output and input pathways of the same nerve are generally separated. Exceptions are the nerves of the funnel, which have many afferents in the same subregions where their motoneurons originate, i.e. the afferents of the anterior funnel nerve run mainly to the palliovisceral and posterior pedal lobes and the afferents of the posterior funnel and collar nerves mainly to the palliovisceral lobe. There is probably a direct feed-back of funnel afferents to their motoneurons; this might be related to the absence of funnel afferents in subregion A where afferents of all other nerves occur.

Afferents of the brachial, pallial and statocyst nerves, which are mostly first-order afferent neurons of receptor cells (Graziadei 1971; Lund 1971; Budelmann & Thies 1977; Colmers 1977, 1981; Budelmann *et al.* 1987) and of the posterior superior (posterior root) and inferior ophthalmic nerves show a widespread distribution in the pedal, palliovisceral and brachial motor output regions. In the pedal lobes (except of the lateral pedal lobes, where only statocyst afferents occur), afferents of each of these nerves are found. No ophthalmic afferents occur in the brachial lobe; conversely, they are most widespread in the palliovisceral lobe. Afferents of the pallial and statocyst nerves occur in both the palliovisceral (many pallial, few statocyst afferents) and brachial lobes.

(ii) *Modalities of sensory input*

Sensory neurons, in general, may be subdivided into two functional categories: (i) neurons that are concerned with the analysis of the world around an animal, and (ii) neurons that play a direct part in the control of posture and movement (Möhl 1985). The first category is comprised of neurons that mediate exteroceptive information of various modalities; the second category includes neurons that mediate proprioceptive information as well as the exteroceptive information that is used to stabilize and align the posture and movement of the body with respect to the environment.

In cephalopods, there are several lines of evidence that the afferent fibres to the motor lobes belong to the second category: (1) *Octopus* receives proprioceptive (stretch) information from its arms, and this information most likely is relayed to the sensory-motor centres (Boycott & Young 1950; Wells 1961); the relay presumably is via afferent fibres of the brachial nerves because their projections

widely correspond with those of the statocyst nerves, which all carry mechanoreceptive information. (2) In the mantle muscles of *Octopus* likely proprioceptors have been described (Sereni & Young 1932; Alexandrowicz 1960; Graziadei 1965; Boyle 1976) as well as proprioceptive features in peripheral nerve fibres of the *Octopus* mantle and *Sepia* fin muscles (Gray 1960; Boyle 1976; Kier *et al.* 1985). (3) There is some evidence for possible proprioceptive afferent fibres in the inferior ophthalmic nerve which innervates the inferior oblique extraocular muscle (Weiss 1984). The afferent projections of the inferior ophthalmic and the pallial nerves widely correspond to those of the brachial and the statocyst nerves (see § 4.b.i); they probably transmit proprioceptive information. (4) Finally, the afferents of the funnel, collar, posterior superior ophthalmic, antorbital, and interbrachial nerves all project to the same regions as do fibres of the statocyst, the brachial and the pallial nerves (see § 4.b.i); quite likely, therefore, they are proprioceptive.

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ABBREVIATIONS USED IN FIGURES

aff.	afferent
art.ceph.	cephalic artery
b.a.	anterior basal lobe
b.d.a.	anterior dorsal basal lobe
b.d.p.	posterior dorsal basal lobe
b.int.	interbasal lobe
b.l.	lateral basal lobe
b.med.	median basal lobe
br.	brachial lobe
br.pr.	prebrachial lobe
buc.p.	posterior buccal lobe
buc.s.	superior buccal lobe
c.br.inf.	infrabrachial commissure
c.br.s.	suprabrachial commissure
c.mag.	magnocellular commissure
c.pe.m.	middle pedal commissure
c.pv.a.	anterior palliovisceral commissure
c.pv.m.	middle palliovisceral commissure
c.pv.p.	posterior palliovisceral commissure
ch.a.	anterior chromatophore lobe
ch.int.con.	interchromatophore connective
ch.p.	posterior chromatophore lobe
con.br.pv.	brachio-palliovisceral connective
eff.	efferent
fr.i.l.	lateral inferior frontal lobe
fr.i.med.	median inferior frontal lobe
fr.s.l.	lateral superior frontal lobe
fr.s.med.	median superior frontal lobe
fun.a.	anterior funnel lobe
fun.p.	posterior funnel lobe
int.br.1	interbrachial lobule 1
int.br.2	interbrachial lobule 2
int.br.3	interbrachial lobule 3
int.br.4	interbrachial lobule 4
mag.d.	dorsal magnocellular lobe
mag.p.	posterior magnocellular lobe

mag.ven.	ventral magnocellular lobe
mag.ven.a.	anterior part of the ventral magnocellular lobe
mag.ven.m.	middle part of the ventral magnocellular lobe
mag.ven.p.	posterior part of the ventral magnocellular lobe
n.br.	brachial nerve
n.br.l.r.	lateral root of the brachial nerve
n.br.med.r.	medial root of the brachial nerve
n.col.	collar nerve
n.fun.a.	anterior funnel nerve
n.fun.p.	posterior funnel nerve
n.op.s.p.r.p.	posterior root of the posterior superior ophthalmic nerve
n.pal.	pallial nerve
n.pal.retr.med.	medial pallial retractor nerve
n.retr.h.	head retractor nerve
n.visc.	visceral nerve
oes.	oesophagus
olf.	olfactory lobe
opt.	optic lobe
pe.a.	anterior pedal lobe
pe.l.a.	anterior lateral pedal lobe
pe.l.p.	posterior lateral pedal lobe
pe.l.p.a.	anterior part of the posterior lateral pedal lobe
pe.l.p.p.	posterior part of the posterior lateral pedal lobe
pe.p.	posterior pedal lobe
ped.	peduncle lobe
pil.cort.e.	extracortical neuropil
prec.	precommissural lobe
pv.	palliovisceral lobe
pv.a.	anterior part of the palliovisceral lobe
pv.dl.	posterodorsal lobe
pv.p.	posterior part of the palliovisceral lobe
sec.	secondary
subfr.	subfrontal lobe
subped.	subpedunculate lobe
subv.	subvertical lobe
subv.a.	anterior subvertical lobe
subv.p.	posterior subvertical lobe
trans.b.med.-prec.	transition region of median basal and precommissural lobes

tr.br.-b.med.	brachial-median basal lobe tract
tr.br.-opt.	brachial-optic lobe tract
vas.d.l.	lateral dorsal vasomotor lobe
vas.d.med.	median dorsal vasomotor lobe
vas.ven.	ventral vasomotor lobe
vas.ven.l.	lateral ventral vasomotor lobe
vas.ven.med.	median ventral vasomotor lobe
vert.	vertical lobe

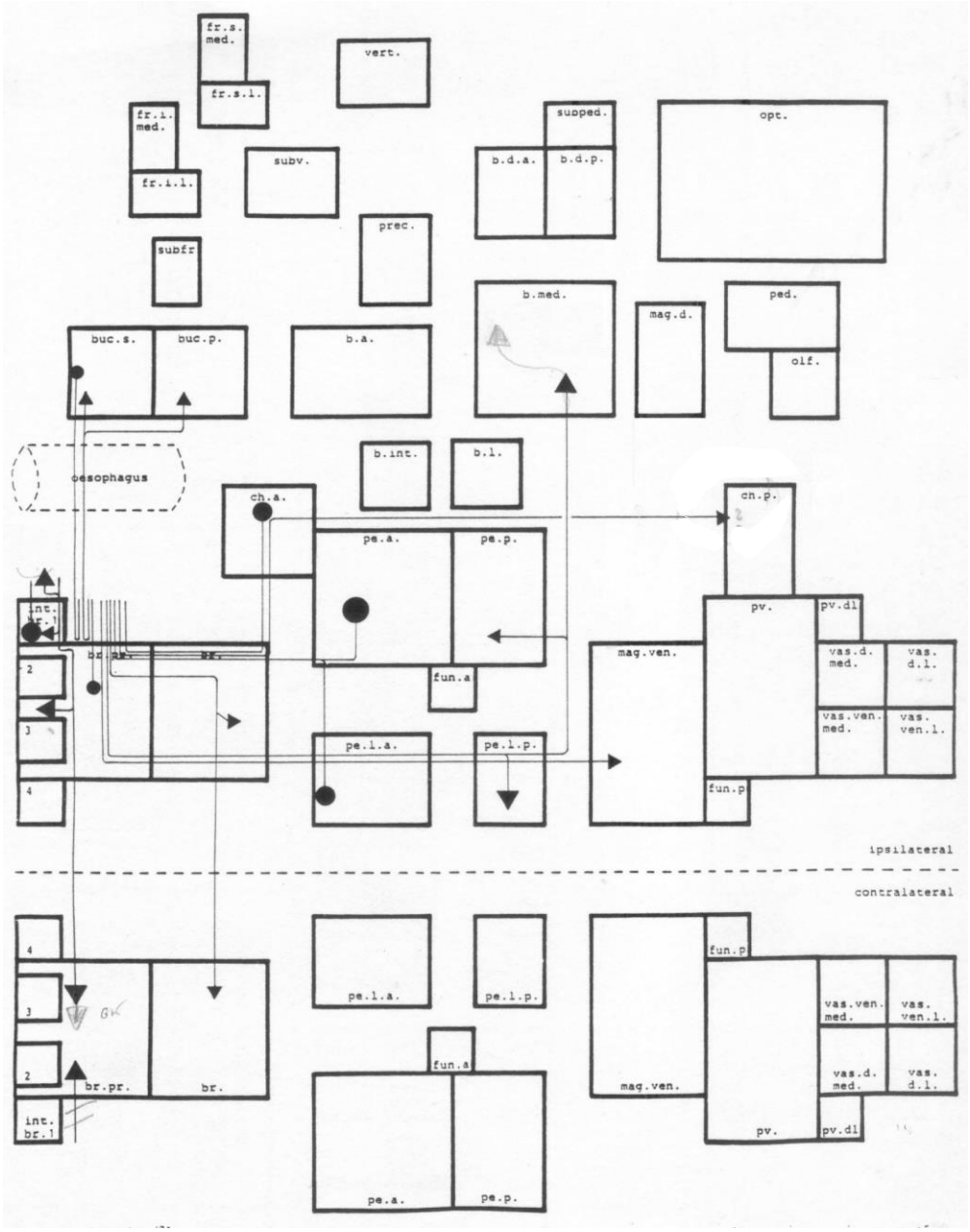

Figure 1. Schematic presentation of the afferent and efferent brain pathways of the superior antorbital nerve of *Octopus vulgaris*, as obtained by centripetal cobalt filling. The rectangles represent the brain lobes as indicated. The relevant contralateral lobes are shown only for the suboesophageal mass of the brain. The sizes of the filled circles or arrowheads provide an approximate indication of the number of the cells or fibres filled. Large filled circles indicate many filled perikarya, small filled circles few. Large arrowheads indicate the termination of many filled afferents, small arrowheads of few. When branched lines are shown they indicate continuation of the pathway, not necessarily of individual fibres. Because of the schematic two-dimensional arrangement of the position of the various brain lobes, the course of the afferent and efferent pathways to their origin or termination does not always represent the actual course present in the brain.

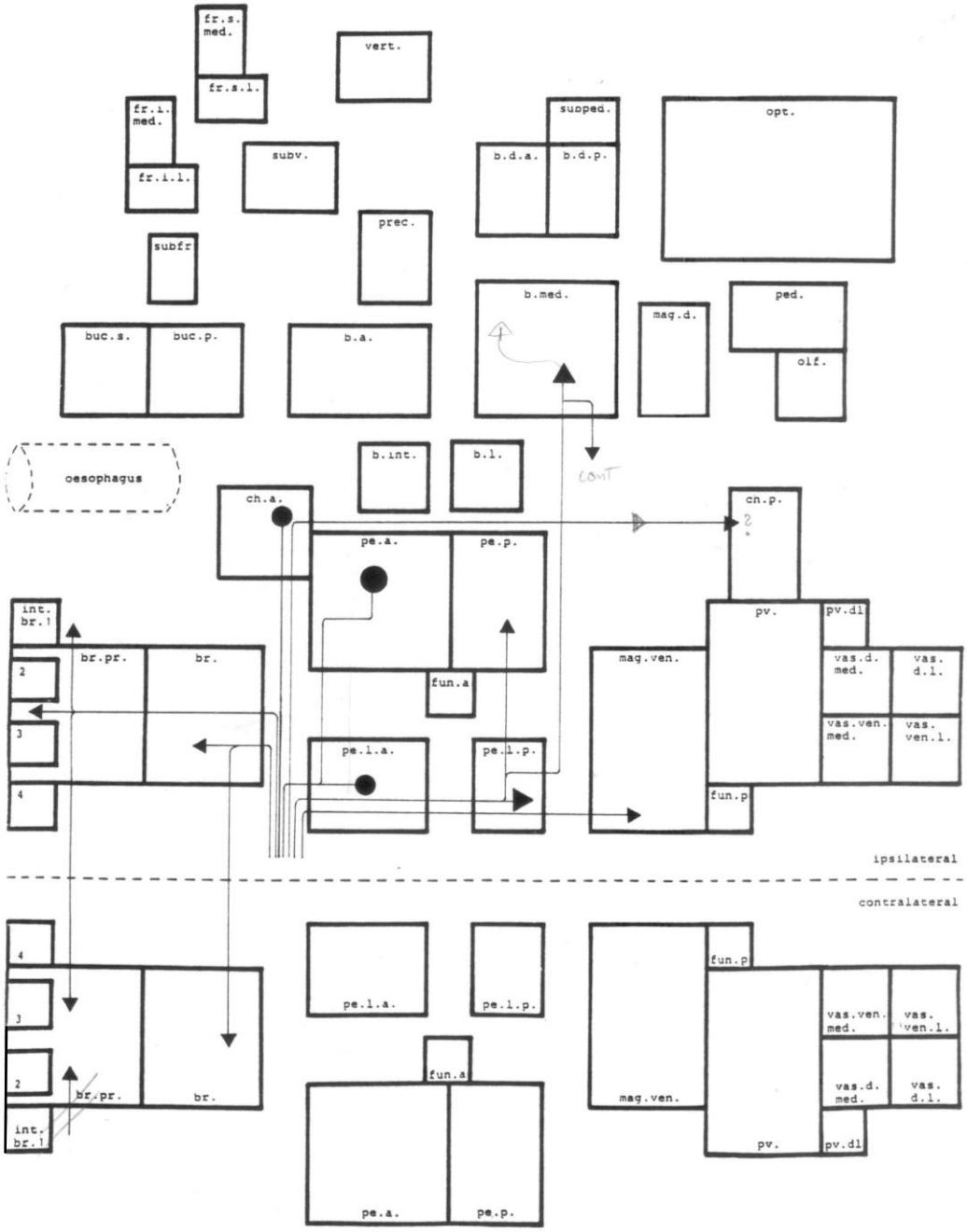

Figure 2. Schematic presentation of the afferent and efferent brain pathways of the inferior antorbital nerve of *Octopus vulgaris*. Conventions as for figure 1.

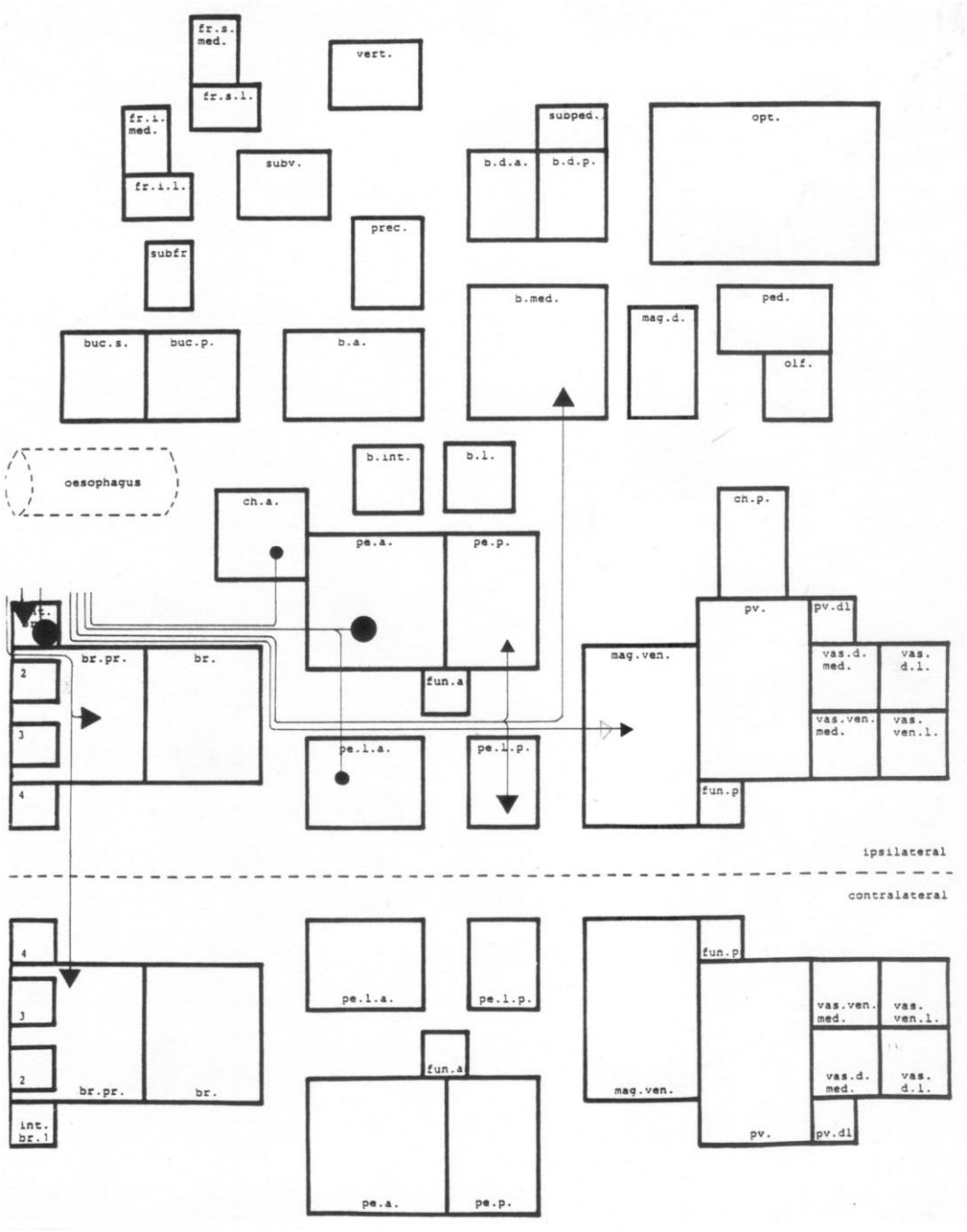

Figure 3. Schematic presentation of the afferent and efferent brain pathways of the first interbrachial nerve of *Octopus vulgaris*. With the exception of the anterior lateral pedal and anterior chromatophore lobes, the termination and origin of fibres apply to the interbrachial nerves 2-4 as well. Conventions as for figure 1.

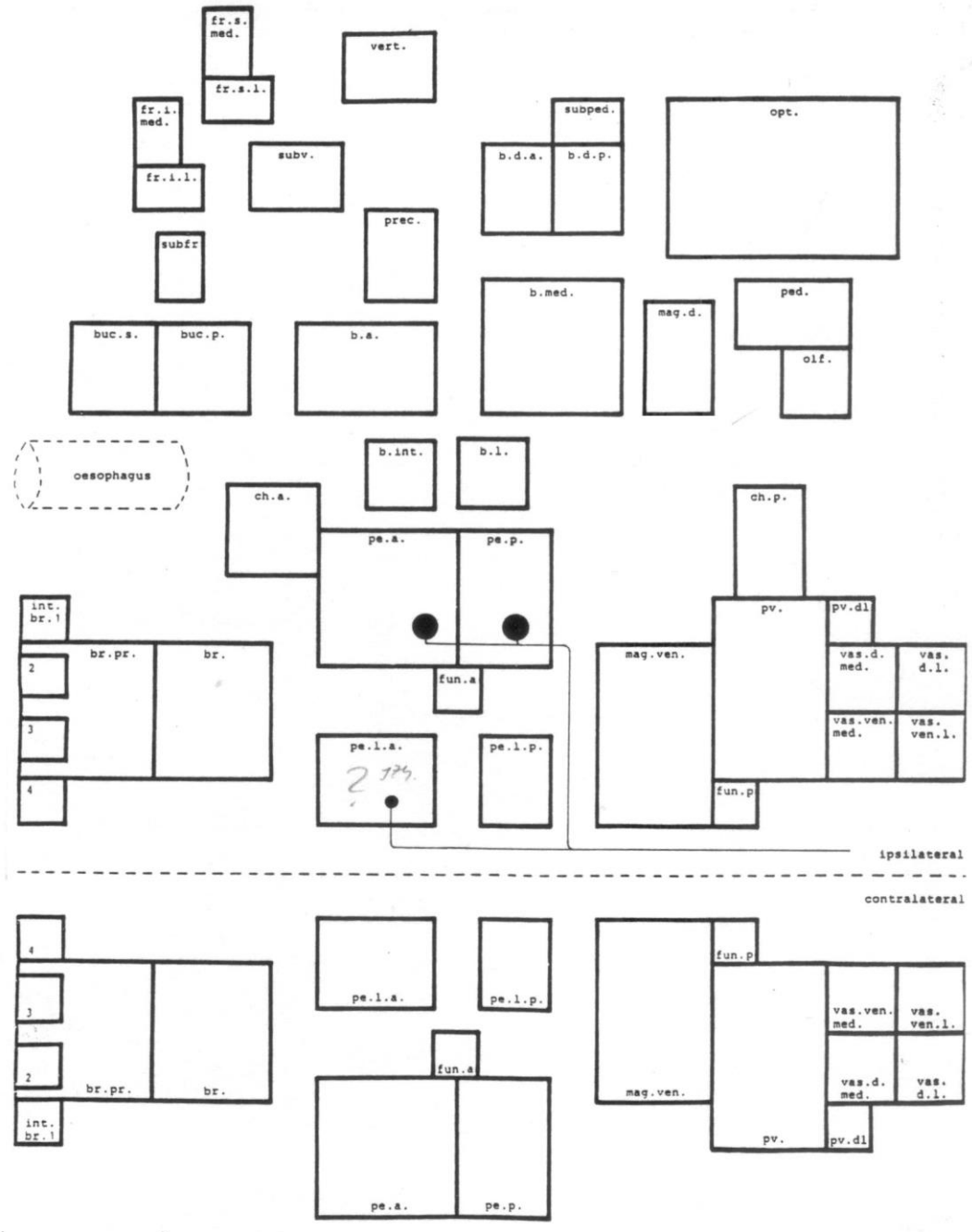

Figure 4. Schematic presentation of the afferent and efferent brain pathways of the anterior and posterior head retractor nerves of *Octopus vulgaris*. Conventions as for figure 1.

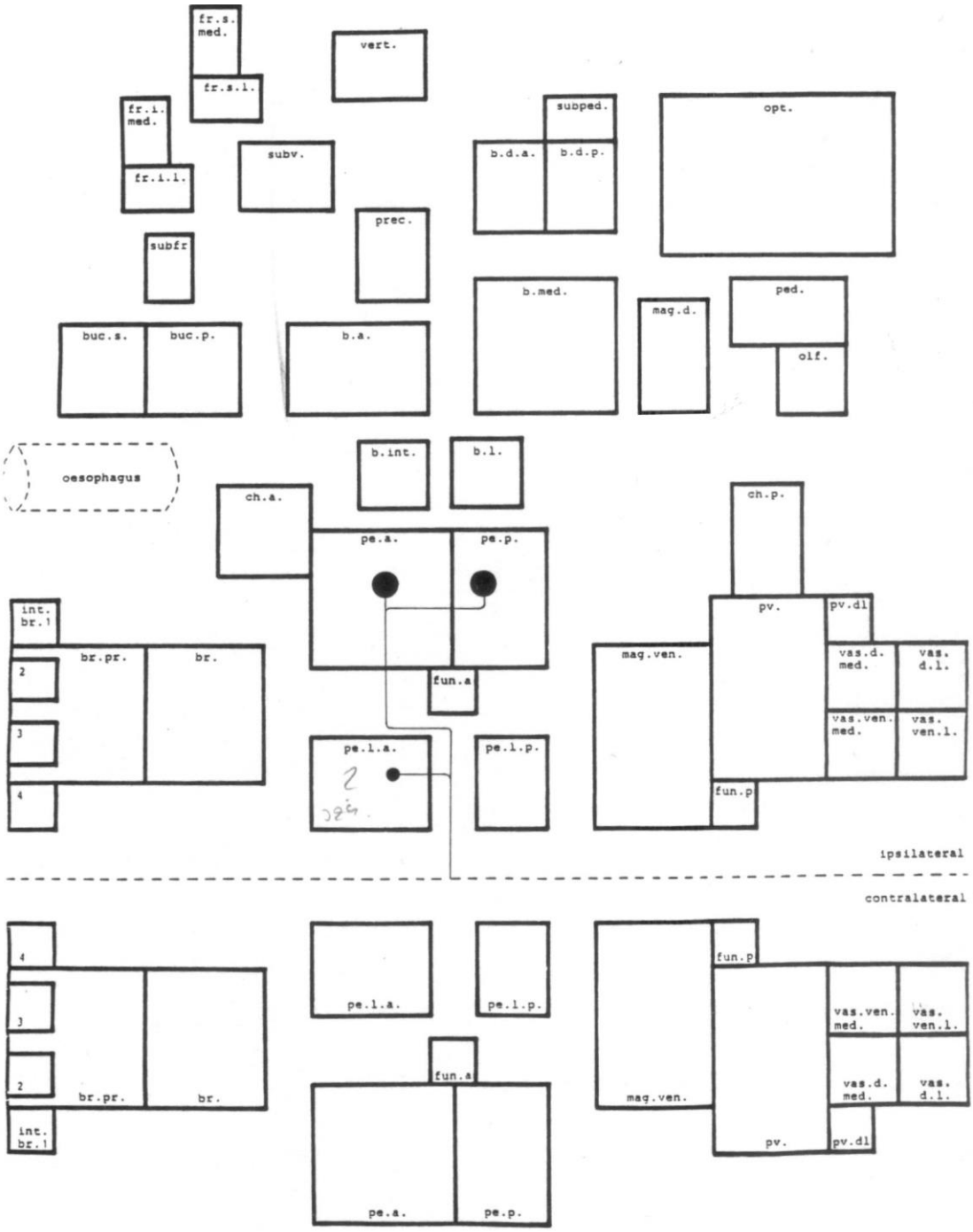

Figure 5. Schematic presentation of the afferent and efferent brain pathways of the medial pallial retractor nerve of *Octopus vulgaris*. Conventions as for figure 1.

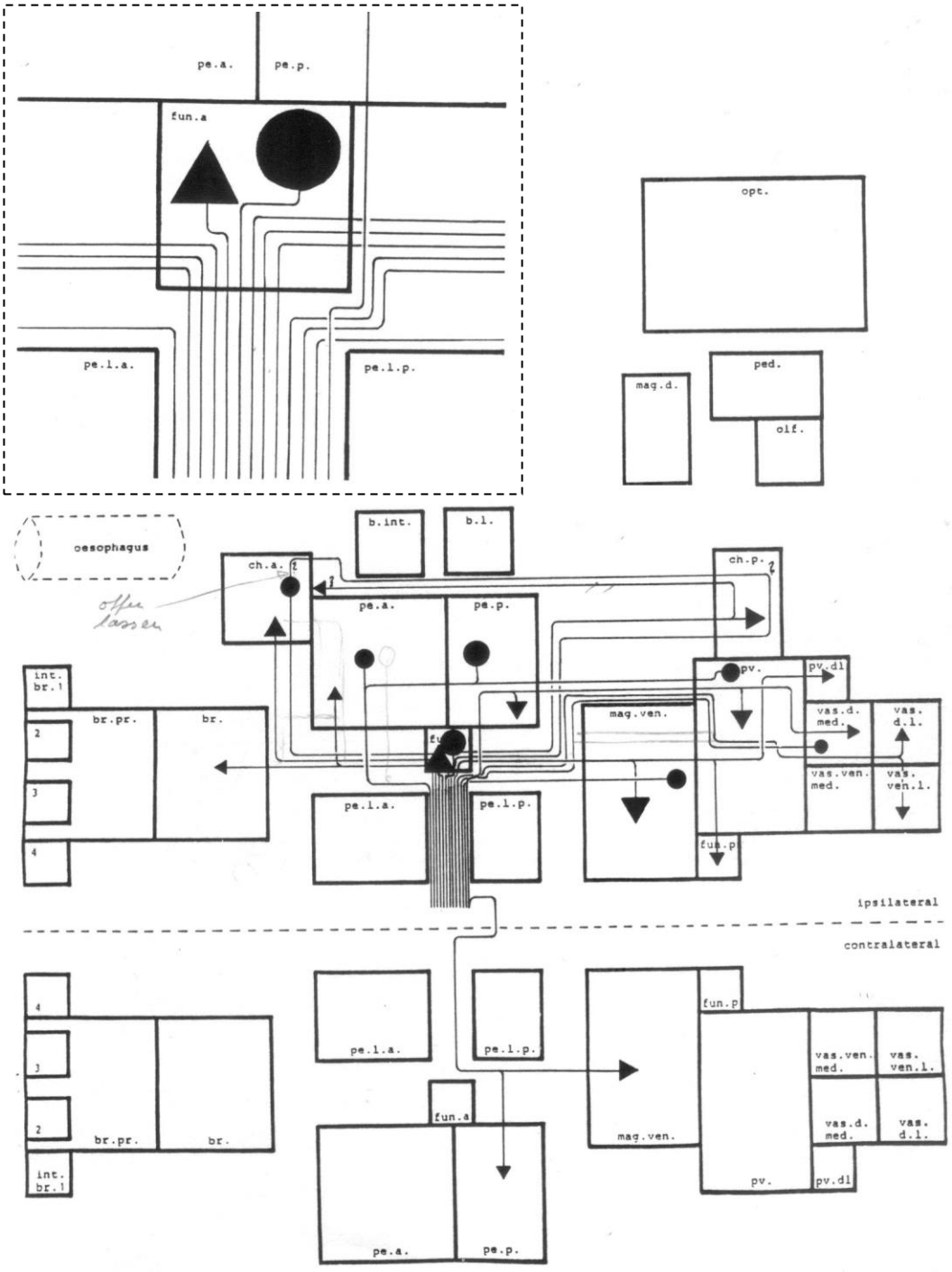

Figure 6. Schematic presentation of the afferent and efferent brain pathways of the anterior funnel nerve of *Octopus vulgaris*. Conventions as for figure 1.

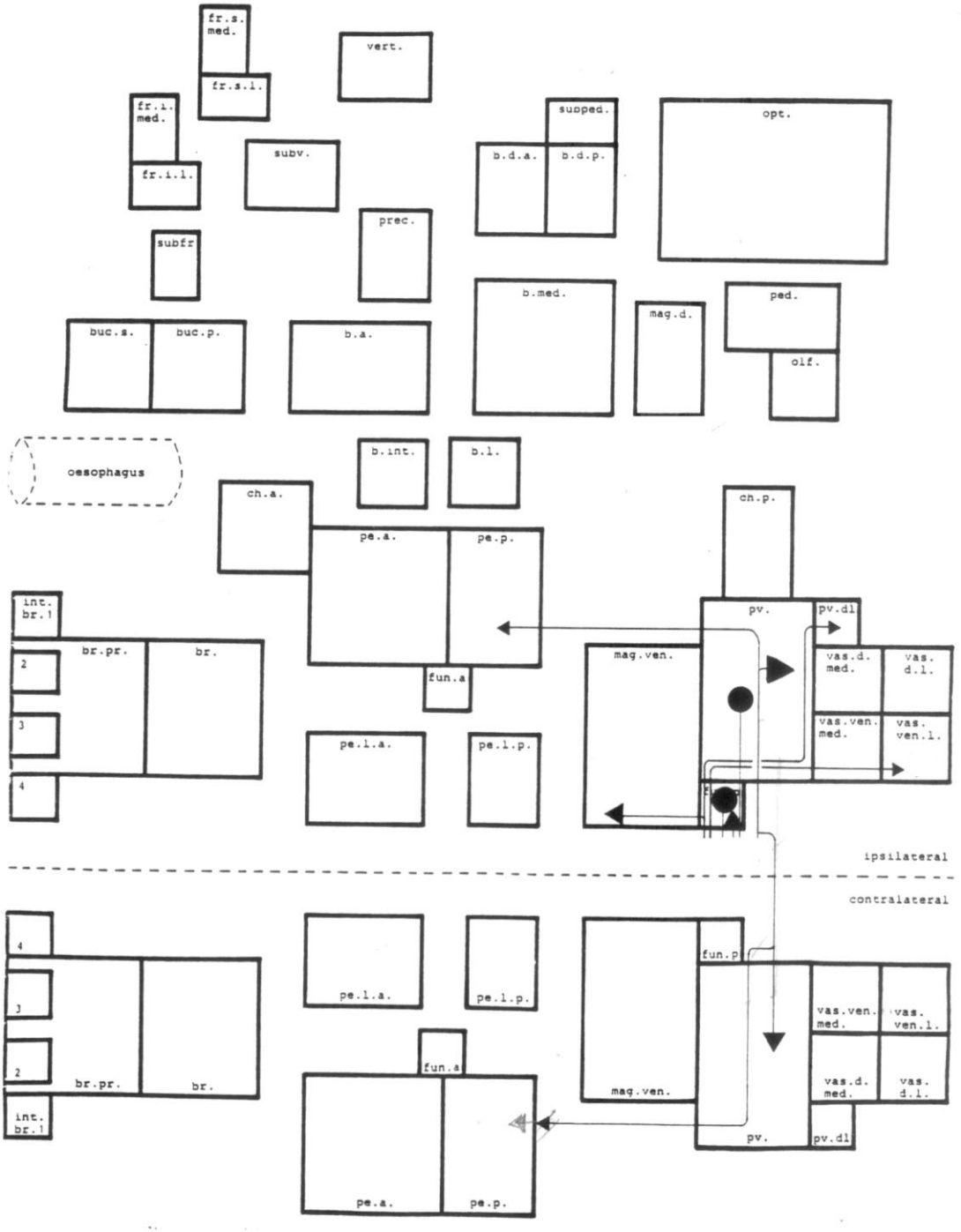

Figure 7. Schematic presentation of the afferent and efferent brain pathways of the posterior funnel nerve of *Octopus vulgaris*. Conventions as for figure 1.

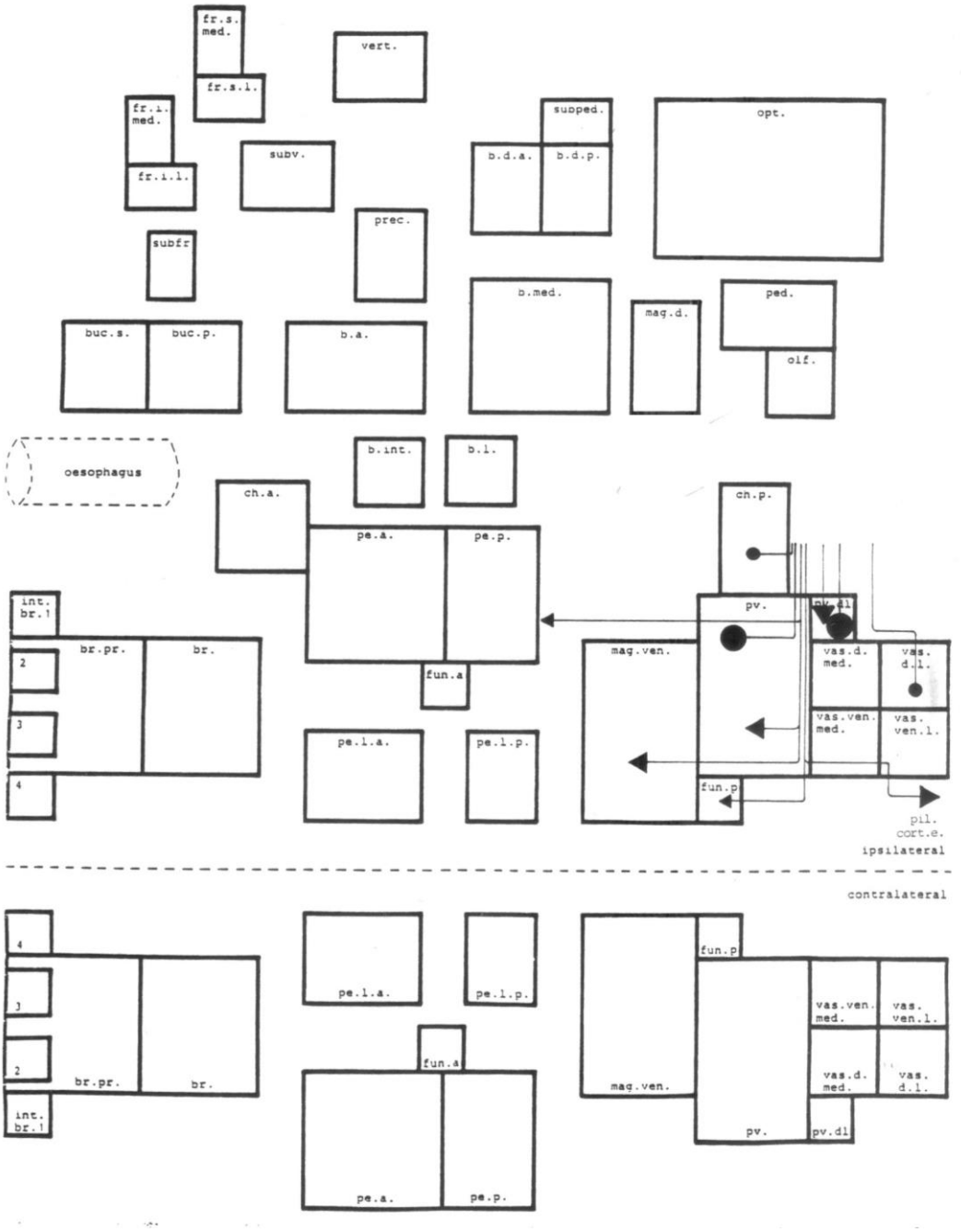

Figure 8. Schematic presentation of the afferent and efferent brain pathways of the collar nerve of *Octopus vulgaris*. Conventions as for figure 1.

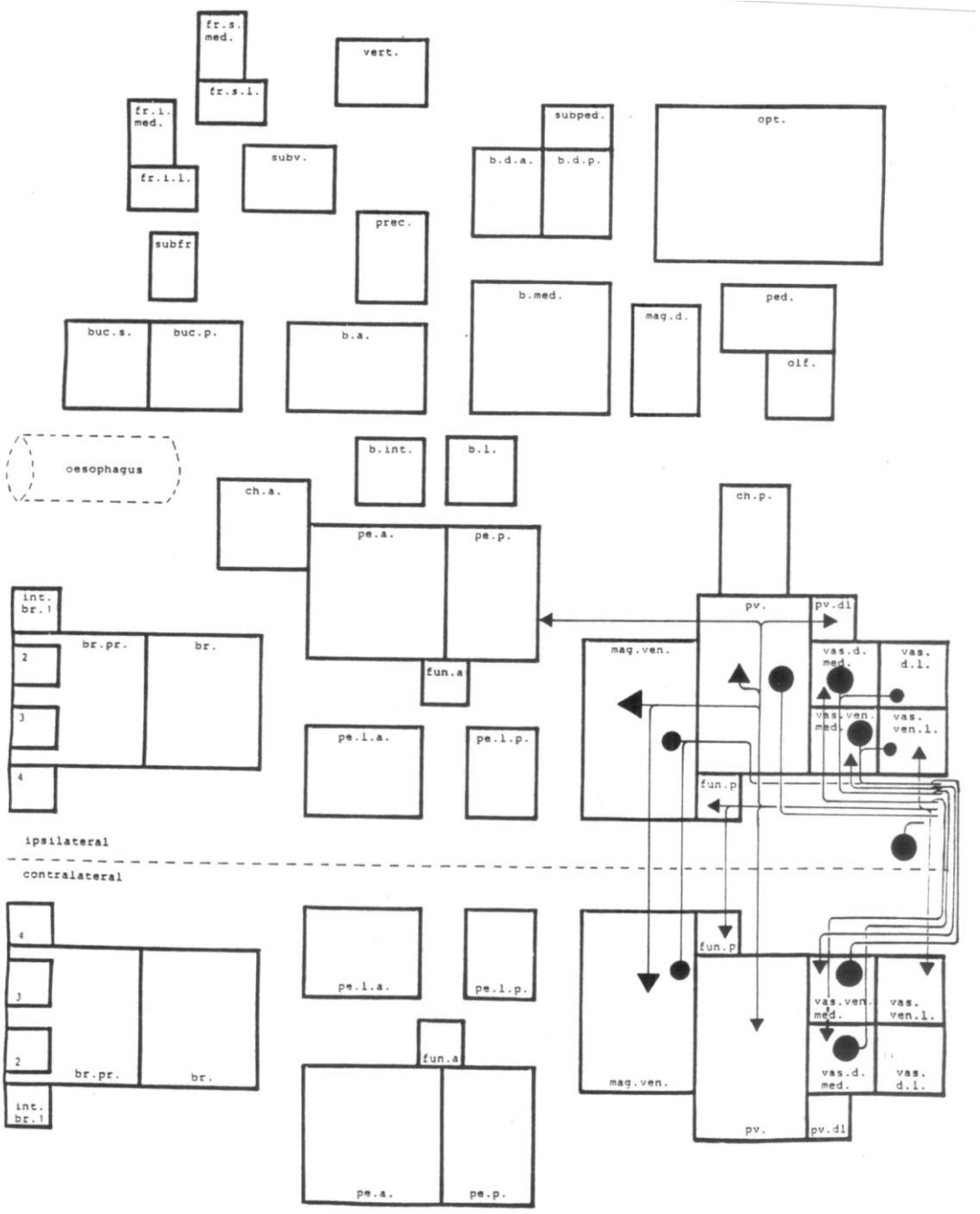

Figure 9. Schematic presentation of the afferent and efferent brain pathways of the visceral nerve of *Octopus vulgaris*. Conventions as for figure 1.

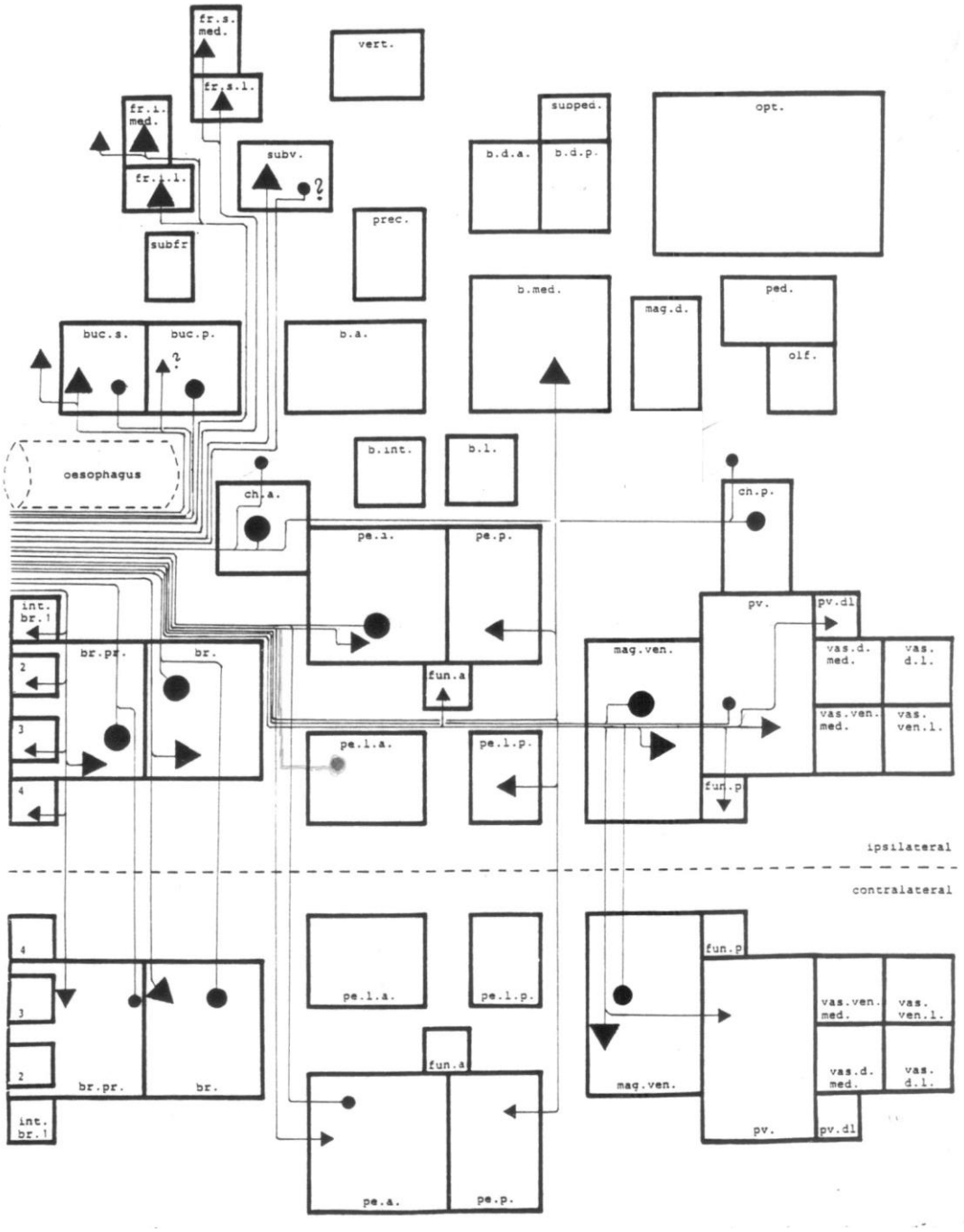

Figure 10. Schematic presentation of the afferent and efferent brain pathways of the third brachial nerve of *Octopus vulgaris*. Conventions as for figure 1.

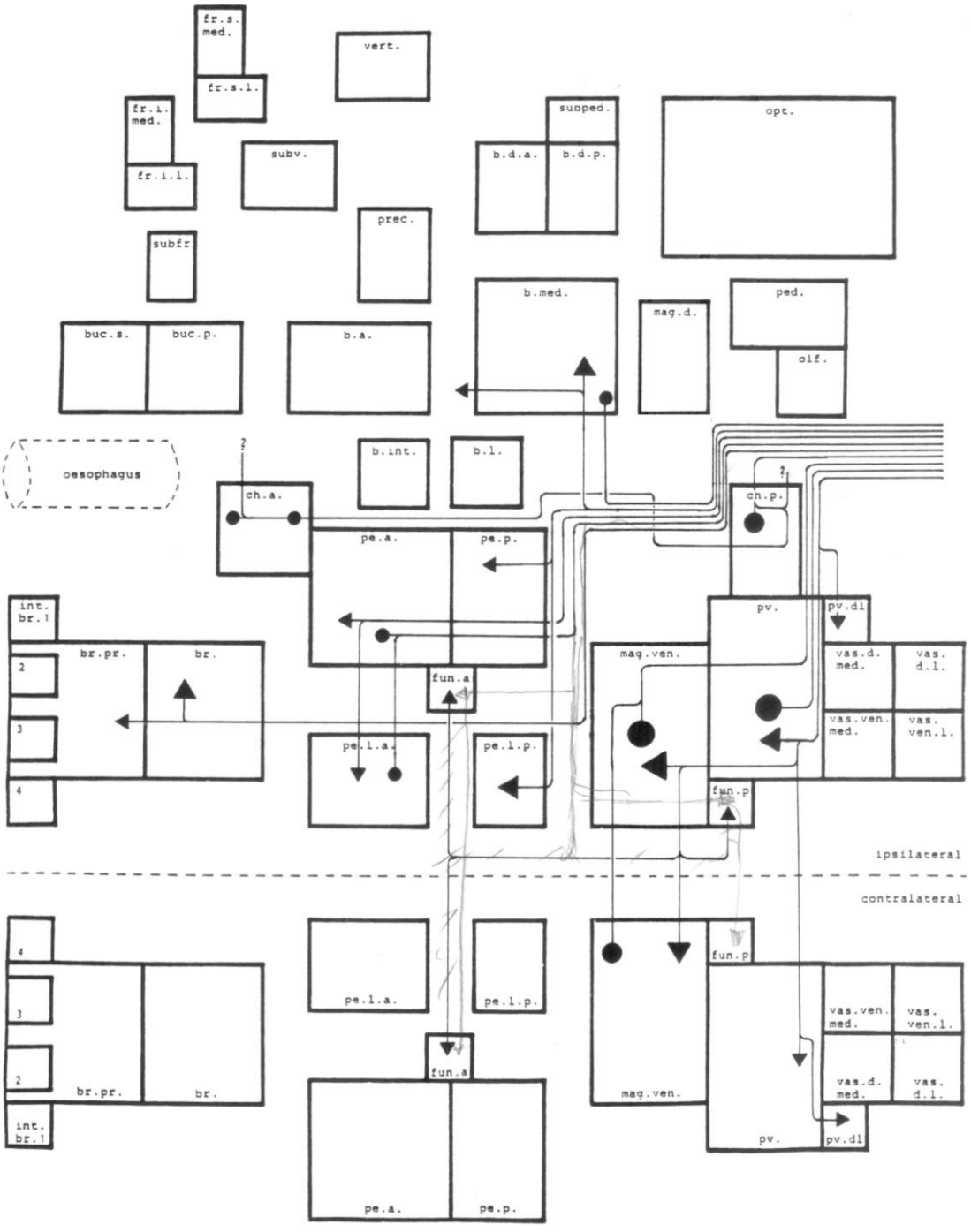

Figure 11. Schematic presentation of the afferent and efferent brain pathways of the pallial nerve of *Octopus vulgaris*. Conventions as for figure 1.

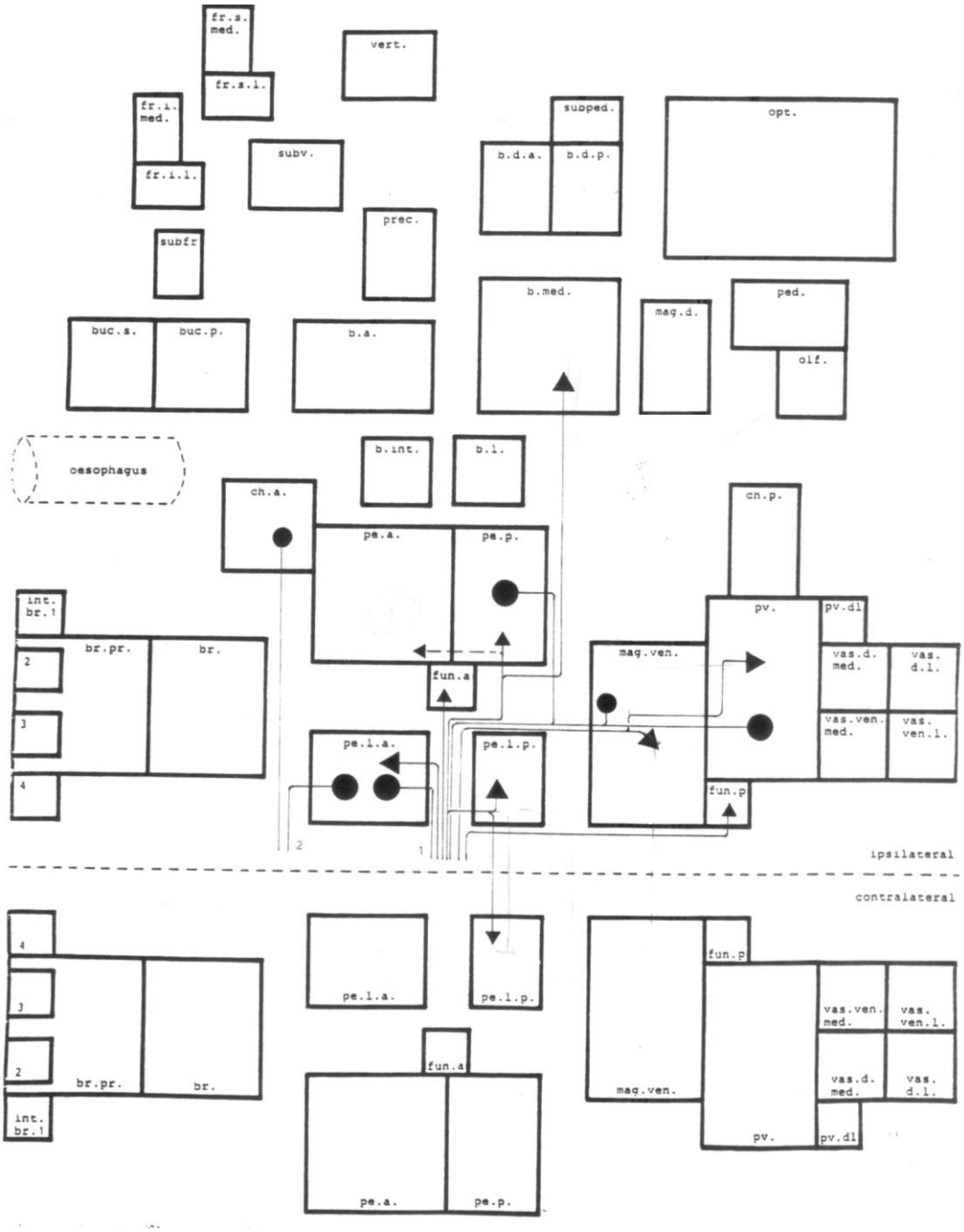

Figure 12. Schematic presentation of the afferent and efferent brain pathways of the inferior ophthalmic and anterior oculomotor nerves of *Octopus vulgaris*. Brain pathways of the posterior root of the posterior superior ophthalmic nerve, and of the remaining oculomotor/ophthalmic nerves largely apply to the inferior ophthalmic and anterior oculomotor nerves, respectively. Conventions as for figure 1.

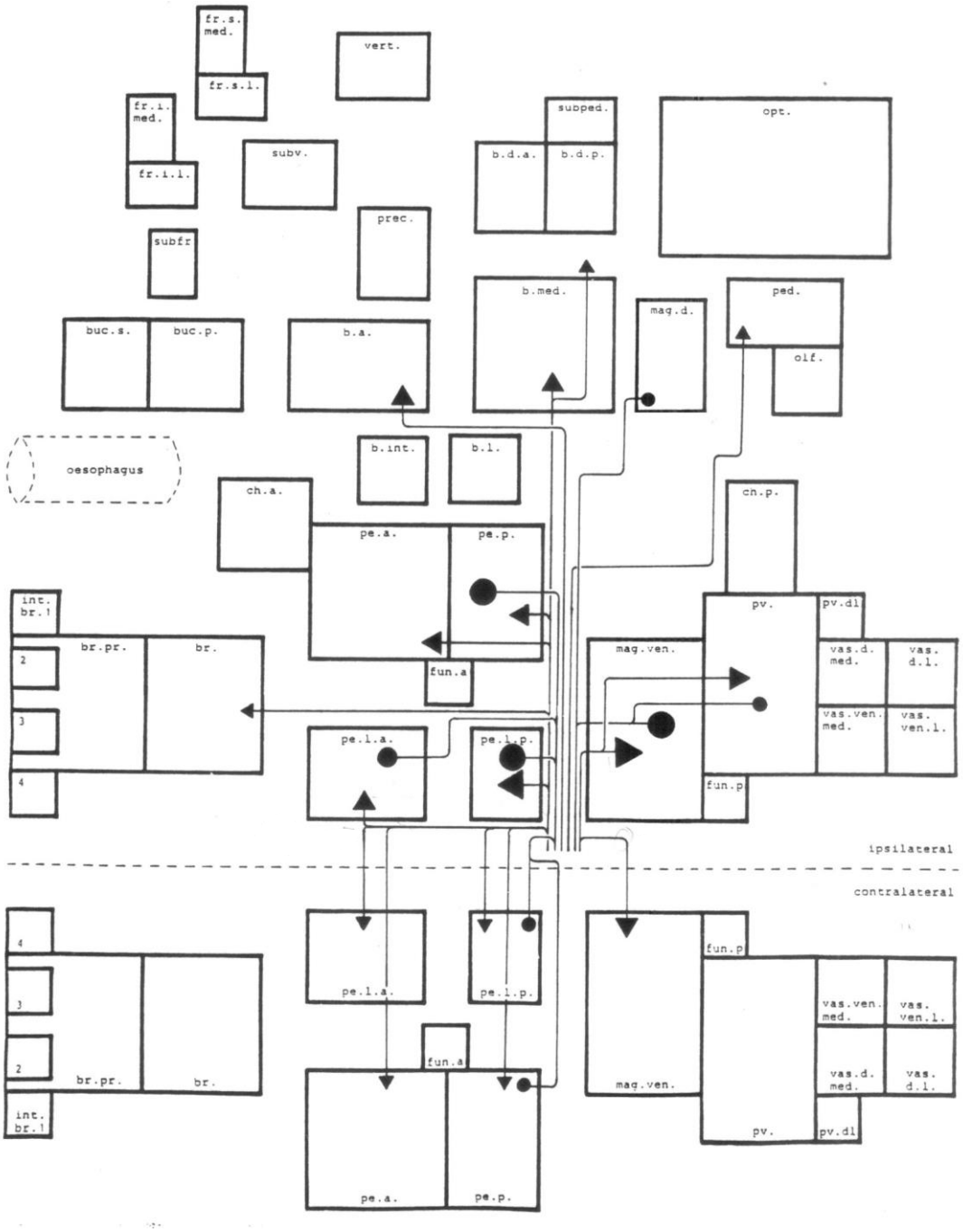

Figure 13. Schematic presentation of the afferent and efferent brain pathways of the posterior crista nerve of *Octopus vulgaris*. Brain pathways largely apply also the macula and middle crista nerves. Conventions as for figure 1.

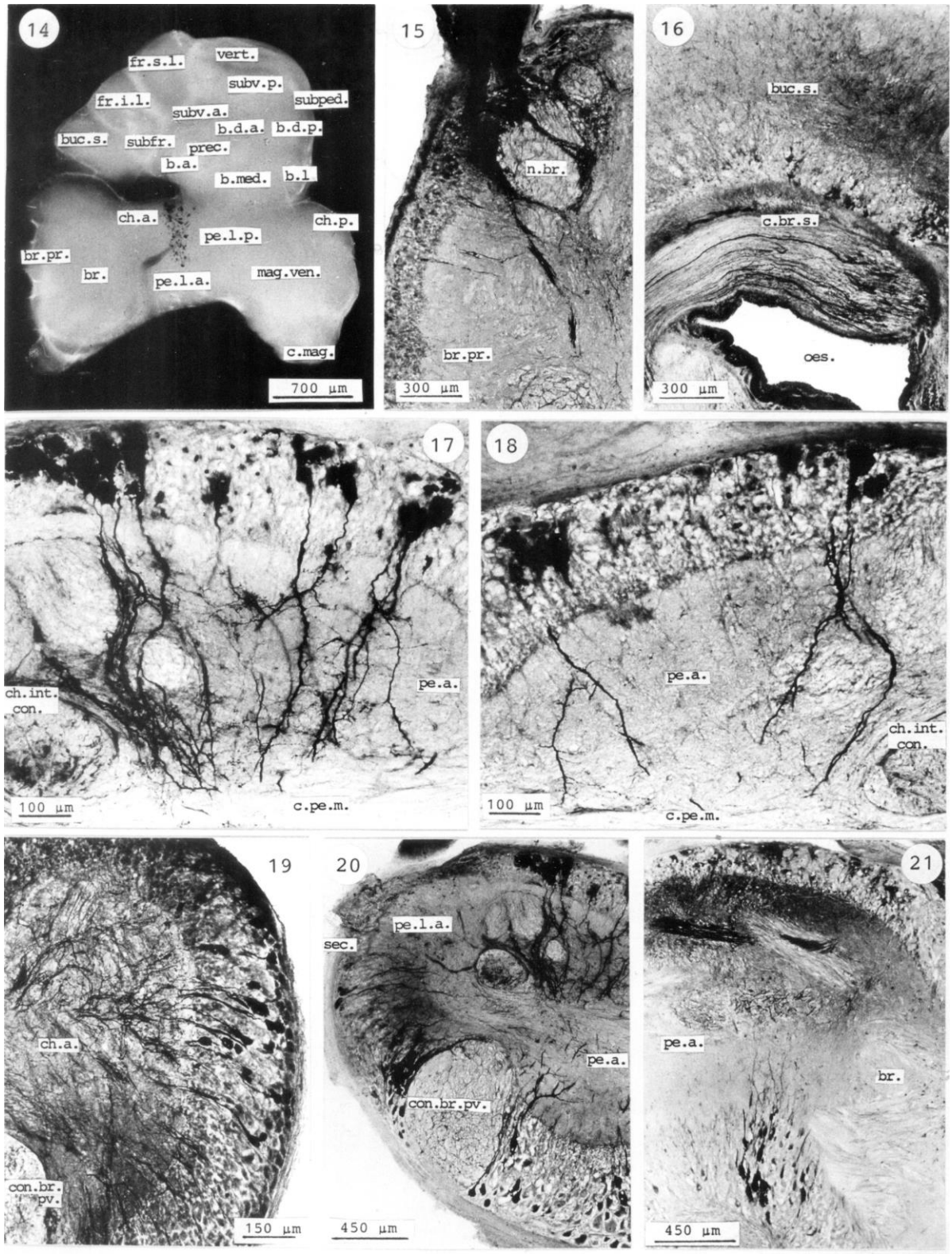
14
fr.s.l.
vert.
subv.p.
fr.i.l.
subped.
subv.a.
b.d.a.
b.d.p.
buc.s.
subfr.
prec.
b.a.
b.med.
b.l
ch.a.
ch.p.
pe.l.p.
br.pr.
br.
pe.l.a.
mag.ven.
c.mag.
700 µm
15
n.br.
br.pr.
300 µm
16
buc.s.
c.br.s.
oes.
300 µm
17
ch.int.
con.
pe.a.
100 µm
c.pe.m.
18
pe.a.
ch.int.
con.
100 µm
c.pe.m.
19
ch.a.
con.br.
pv.
150 µm
20
pe.l.a.
sec.
pe.a.
con.br.pv.
450 µm
21
pe.a.
br.
450 µm

PLATE 1
Figures 14 - 21

Whole mount (figure 14) and transverse (figures 15-20) and sagittal sections (figure 21) of the *Octopus* brain after centripetal cobalt filling of the anterior oculomotor and superior and inferior antorbital nerves.

Figure 14. Lateral view of the brain showing the main lobes. The perikarya in the anterior lateral pedal lobe are stained after centripetal cobalt filling of the posterior branch of the anterior oculomotor nerve that innervates the anterior inferior oblique eye muscle.

Figure 15. Perikarya and afferent fibres in the prebrachial lobe and first interbrachial lobule after filling of the superior antorbital nerve.

Figure 16. Perikarya in the superior buccal lobe and afferent fibres in the suprabrachial commissure crossing to the contralateral side after filling of the superior antorbital nerve.

Figures 17 and 18. Perikarya in the dorsal anterior pedal lobe after filling of the inferior antorbital nerve.

Figure 19. Perikarya in the anterior chromatophore lobe after filling of the inferior antorbital nerve. (Perikarya of the superior antorbital and first interbrachial nerves show similar distributions).

Figure 20. Perikarya in the anterior pedal and anterior lateral pedal lobes after filling of the inferior antorbital nerve. Single secondarily filled neurons (arrows) occur in the anterior lateral pedal lobe. (Perikarya of the superior antorbital, interbrachial, medial pallial retractor and head retractor nerves show similar distributions).

Figure 21. Perikarya in the anterior pedal lobe and an afferent fibre bundle running to the posterior lateral pedal and median basal lobes after filling of the superior antorbital nerve. (Perikarya of the inferior antorbital and interbrachial nerves show similar distributions).

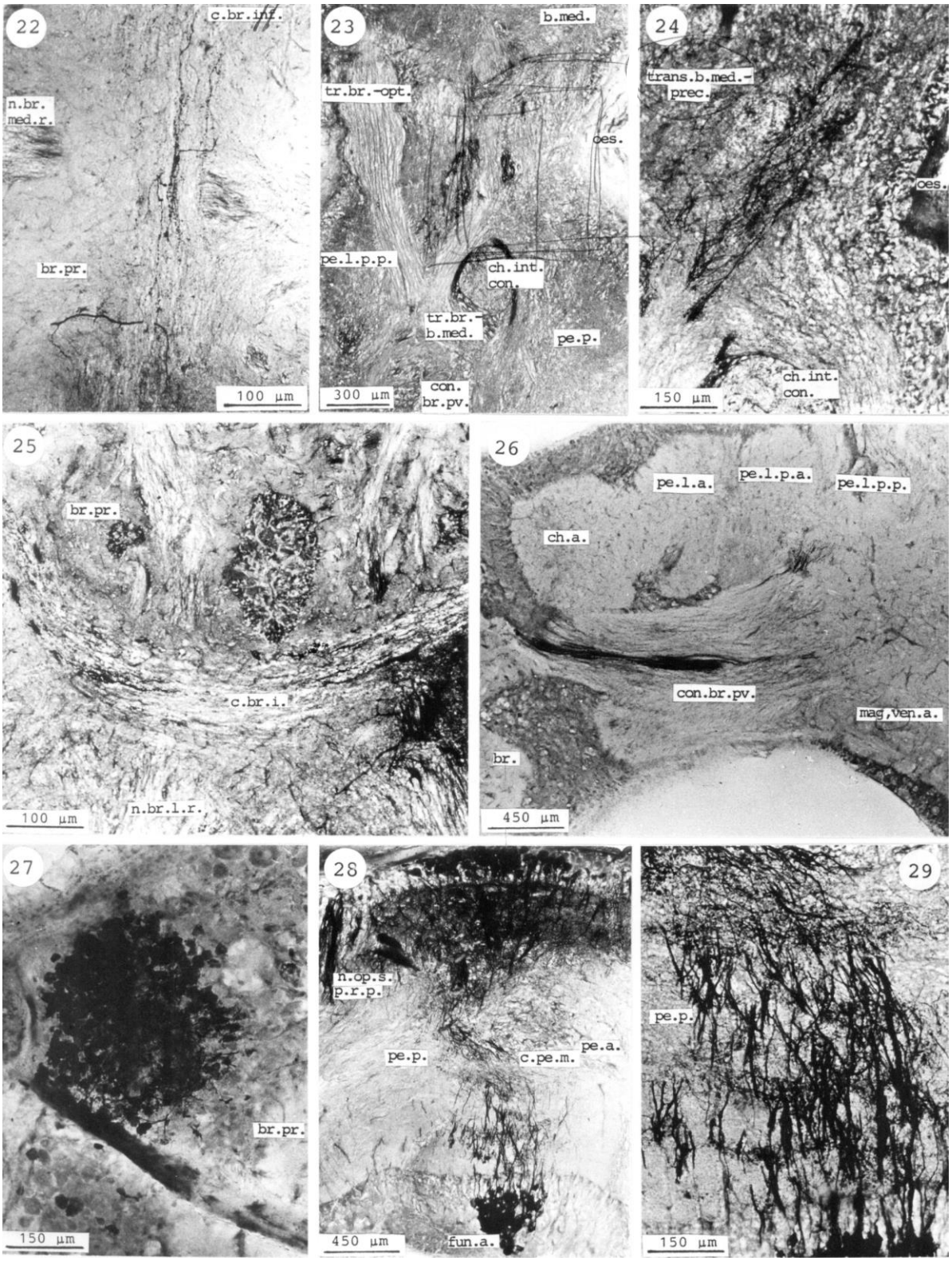
22
c.br.inf.
n.br.
med.r.
br.pr.
100 µm
23
b.med.
tr.br.-opt.
oes.
pe.l.p.p.
ch.int.
con.
tr.br.-
b.med.
pe.p.
con.
br.pv.
300 µm
24
trans.b.med.-
prec.
oes.
ch.int.
con.
150 µm
25
br.pr.
c.br.i.
100 µm
n.br.l.r.
26
pe.l.a.
pe.l.p.a.
pe.l.p.p.
ch.a.
con.br.pv.
mag,ven.a.
br.
450 µm
27
br.pr.
150 µm
28
n.op.s.
p.r.p.
pe.p.
c.pe.m.
pe.a.
450 µm
fun.a.
29
pe.p.
150 µm

PLATE 2
Figures 22 - 29

Sagittal (figures 22 and 26-29) and transverse (figures 23-25) sections of the anterior and middle suboesophageal mass of the *Octopus* brain after centripetal cobalt filling of the interbrachial, anterior head retractor, superior, and inferior antorbital nerves.

Figure 22. Afferent fibres in the prebrachial lobe and infrabrachial commissure after filling of the third interbrachial nerve. (Afferent fibres of the other interbrachial and the antorbital nerves show similar distributions).

Figures 23 and 24. Afferent fibres in the posterior pedal and posterior lateral pedal lobes and the transition region of the precommissural and median basal lobes after filling of the superior and inferior antorbital nerves. (Afferent fibres of the interbrachial nerves show similar distributions).

Figure 25. Afferent fibres in the prebrachial lobe and infrabrachial commissure after filling of the inferior antorbital nerve. (Afferent fibres of the superior antorbital and interbrachial nerves show similar distributions).

Figure 26. Afferent fibres in the brachio-palliovisceral connective, running to the posterior lateral pedal and ventral magnocellular lobes, after filling of the second interbrachial nerve. (Afferent fibres of the other interbrachial nerves and the antorbital nerves show similar distributions).

Figure 27. Perikarya in the second interbrachial lobule after filling of the second interbrachial nerve. (Perikarya of the other interbrachial nerves show similar distributions in their respective lobules).

Figures 28 and 29. Efferents and their overlapping collaterals in the anterior and posterior pedal lobes after filling of the anterior head retractor nerve. (Efferents of the medial pallial retractor nerve show similar distribution).

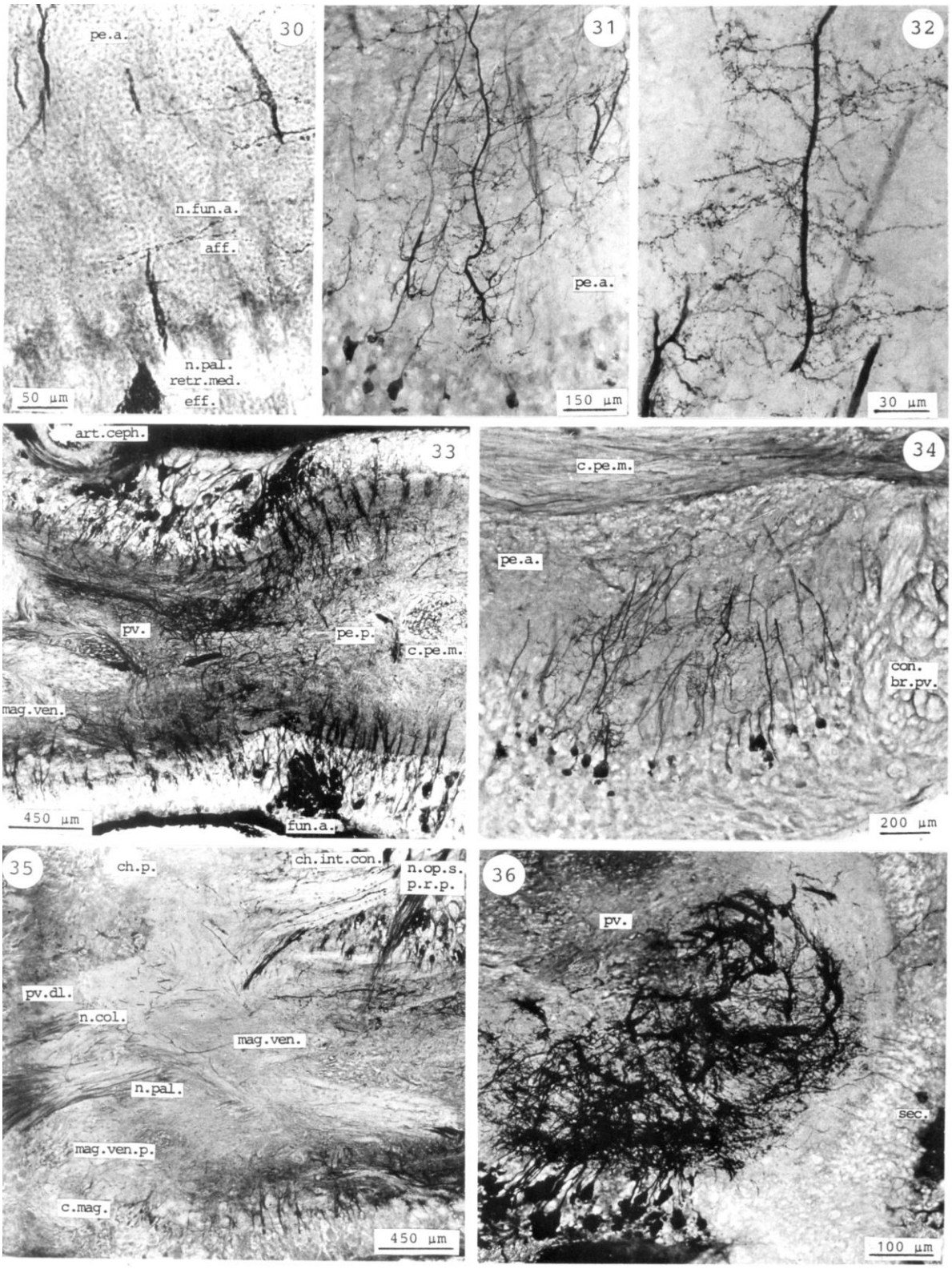
30
pe.a.
n.fun.a.
aff.
n.pal.
retr.med.
eff.
50 µm
31
pe.a.
150 µm
32
30 µm
33
art.ceph.
pv.
pe.p.
c.pe.m.
mag.ven.
450 µm
fun.a.
34
c.pe.m.
pe.a.
con.
br.pv.
200 µm
35
ch.p.
ch.int.con.
n.op.s.
p.r.p.
pv.dl.
n.col.
mag.ven.
n.pal.
mag.ven.p.
c.mag.
450 µm
36
pv.
sec.
100 µm

PLATE 3
Figures 30 - 36

Transverse (figures 30-32 and 34), sagittal (figures 33 and 35) and oblique sagittal (figure 36) sections of the middle and posterior suboesophageal mass of the *Octopus* brain after centripetal cobalt filling of the medial pallial retractor, posterior head retractor, and anterior and posterior funnel nerves.

Figure 30. Efferent and varicose afferent fibres in the ventral pedal lobe, at the level of the middle pedal commissure, after centripetal cobalt double filling of the anterior funnel and medial pallial retractor nerves.

Figures 31 and 32. Efferents in the ventral pedal lobe, at the level of the middle pedal commissure, after filling of the posterior head retractor nerve. Their trunks show many fine collateral fibres, some perhaps with terminal bushes.

Figure 33. Perikarya and afferent fibres in the posterior pedal, anterior palliovisceral and anterior funnel lobes after filling of the anterior funnel nerve.

Figure 34. Perikarya in the ventral anterior pedal lobe, at the level of the middle pedal commissure, after filling of the posterior head retractor nerve. (Perikarya of the medial pallial retractor nerve show similar distribution).

Figure 35. Varicose afferent fibres in the interchromatophore connective and ventral magnocellular lobes, at the level of entry of the collar and pallial nerves, after filling of the anterior funnel nerve.

Figure 36. Perikarya and bundled afferent fibres in the anterior palliovisceral lobe after filling of the posterior funnel nerve. Medially, a secondarily filled neuron (arrow). (Perikarya of the anterior funnel nerve show similar distribution).

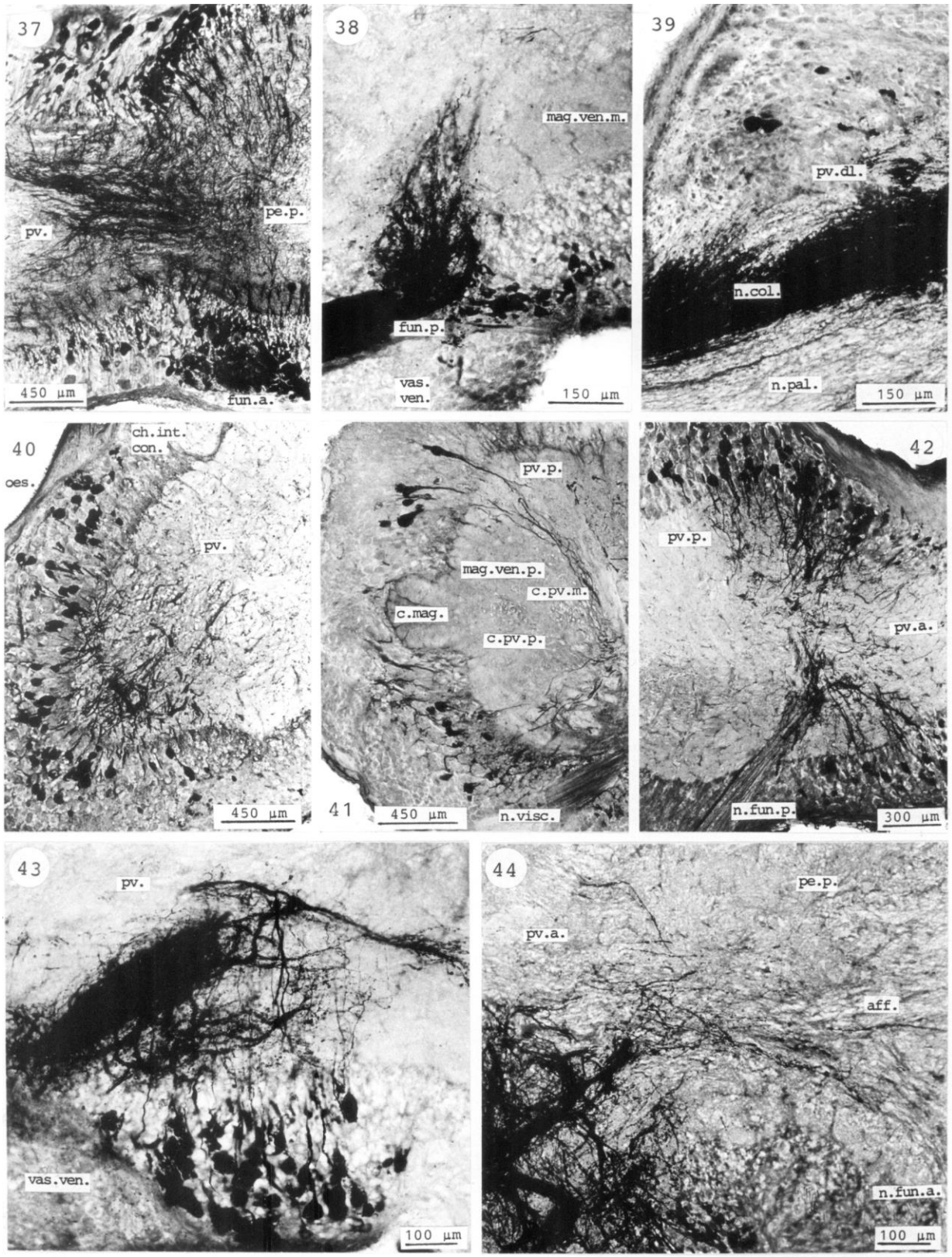
37
pe.p.
pv.
450 µm
fun.a.
38
mag.ven.m.
fun.p.
vas.
ven.
150 µm
39
pv.dl.
n.col.
n.pal.
150 µm
40
ch.int.
con.
oes.
pv.
450 µm
41
pv.p.
mag.ven.p.
c.pv.m.
c.mag.
c.pv.p.
450 µm
n.visc.
42
pv.p.
pv.a.
n.fun.p.
300 µm
43
pv.
vas.ven.
100 µm
44
pe.p.
pv.a.
aff.
n.fun.a.
100 µm

PLATE 4
Figures 37 - 44

Sagittal (figures 37-39 and 41-44) and transverse (figure 40) sections of the middle and posterior suboesophageal mass of the *Octopus* brain after centripetal cobalt filling of the collar, and anterior and posterior funnel nerves.

Figure 37. Perikarya in the posterior pedal, anterior palliovisceral and anterior funnel lobes after filling of the anterior funnel nerve.

Figure 38. Perikarya and afferent fibres in the posterior funnel and ventral magnocellular lobes after filling of the posterior funnel nerve.

Figure 39. Perikarya and afferent fibres in the posterodorsal lobe after filling of the collar nerve.

Figure 40. Perikarya and afferent fibres in the anterior palliovisceral lobe after filling of the posterior funnel nerve. (Perikarya of the anterior funnel, collar and visceral nerves show similar distributions).

Figure 41. Perikarya in the medial posterior ventral magnocellular lobe, between the lateral and medial dorsal and ventral vasomotor lobes, after filling of the anterior funnel nerve. (Perikarya of the brachial and pallial nerves show similar distributions).

Figure 42. Perikarya and afferent fibres in the palliovisceral lobe after filling of the collar nerve. (Perikarya of the visceral nerve show similar distributions).

Figures 43 and 44. Perikarya and afferent fibres in the lateral palliovisceral lobe after filling of the posterior funnel nerve. Some afferents run anteriorly in the posterior pedal lobe to the palliovisceral branch of the anterior funnel nerve (figure 44), as do afferents of the collar nerve.

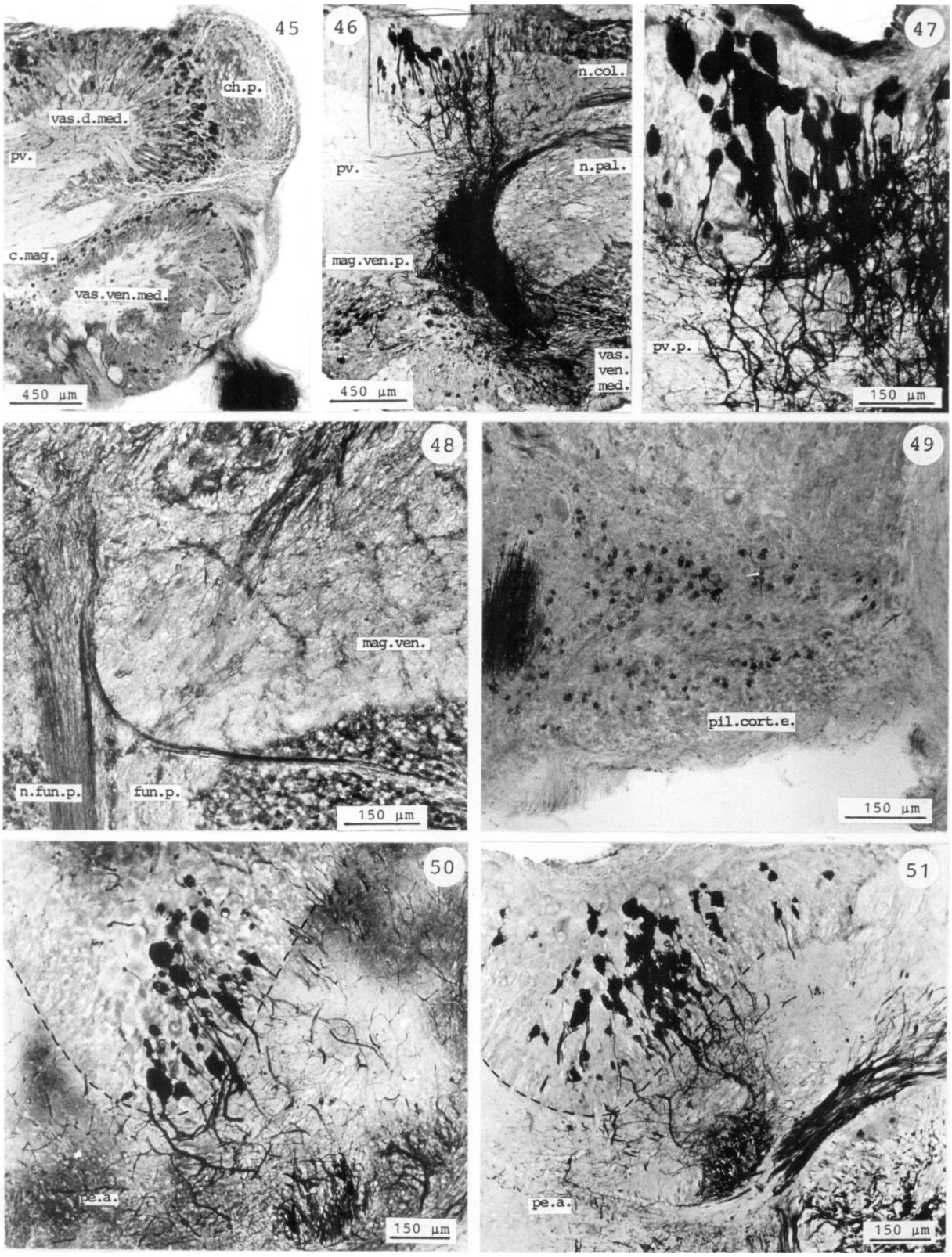
45
ch.p.
vas.d.med.
pv.
c.mag.
vas.ven.med.
450 µm
46
n.col.
pv.
n.pal.
mag.ven.p.
vas.
ven.
med.
450 µm
47
pv.p.
150 µm
48
mag.ven.
n.fun.p.
fun.p.
150 µm
49
pil.cort.e.
150 µm
50
pe.a.
150 µm
51
pe.a.
150 µm

PLATE 5
Figures 45 - 51

Oblique transverse (figures 45-47) and transverse (figures 48-51) sections of the middle and posterior suboesophageal mass of the *Octopus* brain after centripetal cobalt filling of the collar, visceral, and third and fourth brachial nerves.

Figure 45. Perikarya in the median dorsal and ventral vasomotor lobes after filling of the visceral nerve.

Figures 46 and 47. Perikarya and afferent fibres in the median ventral vasomotor, posterior ventral magnocellular and palliovisceral lobes after filling of the visceral nerve. Bundles of afferent fibres run to the entry of the pallial and collar nerves.

Figure 48. Afferent fibre bundles in the continuous neuropil of the ventral magnocellular and posterior funnel lobes after filling of the collar nerve. The bundle proceeds into the extracortical neuropil.

Figure 49. Perikarya in the extracortical neuropil below the median ventral vasomotor lobe, after filling of the visceral nerve.

Figures 50 and 51. Perikarya in the anterior pedal lobes after filling of the fourth and third brachial nerves, respectively. The perikarya of the fourth brachial nerve (figure 50) cluster more medially than those of the third brachial nerve (figure 51) (vertical lines indicate midline).

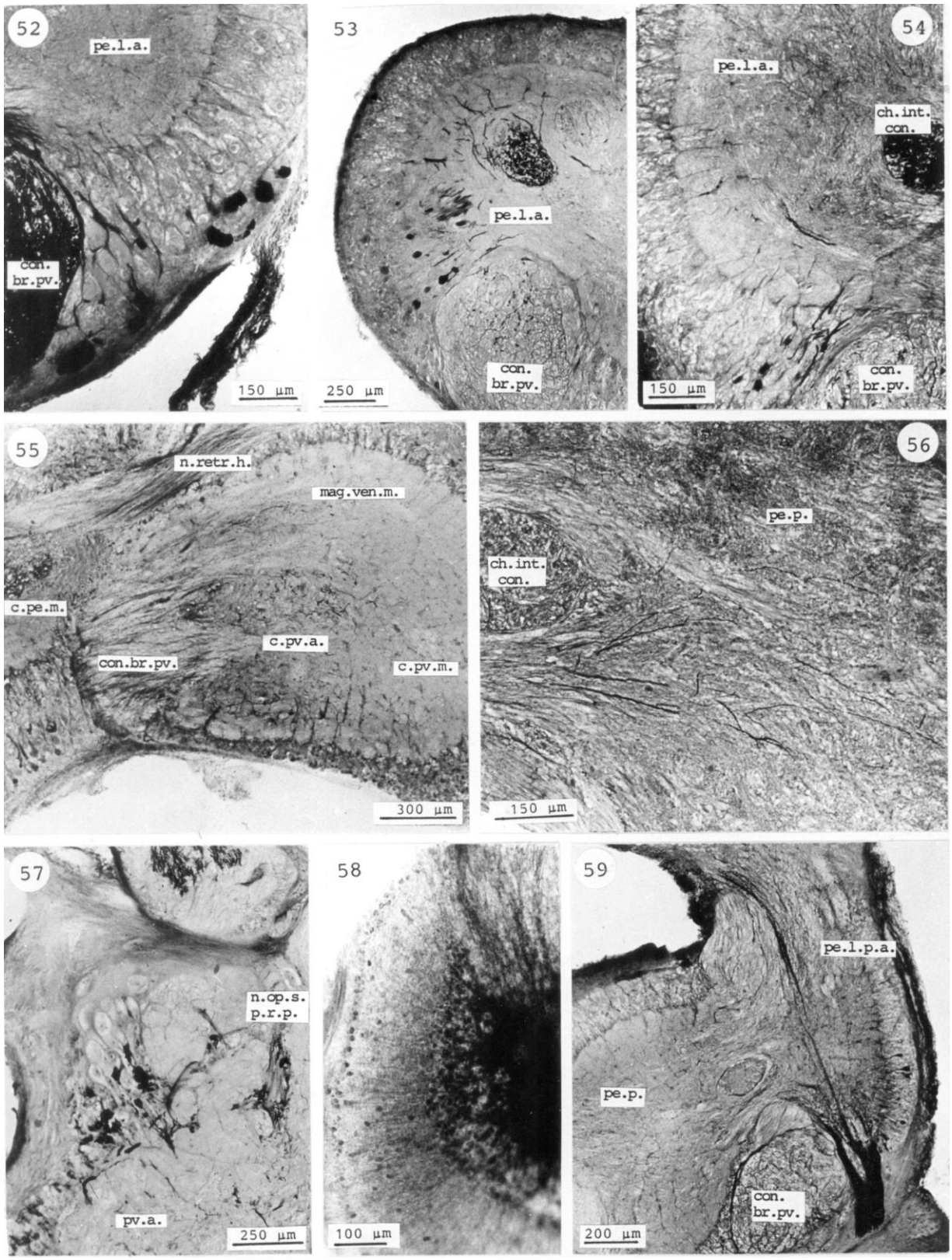
52
pe.l.a.
con.
br.pv.
150 µm
53
pe.l.a.
con.
br.pv.
250 µm
54
pe.l.a.
ch.int.
con.
con.
br.pv.
150 µm
55
n.retr.h.
mag.ven.m.
c.pe.m.
c.pv.a.
con.br.pv.
c.pv.m.
300 µm
56
pe.p.
ch.int.
con.
150 µm
57
n.op.s.
p.r.p.
pv.a.
250 µm
58
100 µm
59
pe.l.p.a.
pe.p.
con.
br.pv.
200 µm

PLATE 6
Figures 52 - 59

Transverse (figures 52-54, 56, 57 and 59) and sagittal (figure 55) sections of the middle and posterior suboesophageal mass of the *Octopus* brain after centripetal cobalt fillings of the brachial, pallial, anterior oculomotor, inferior ophthalmic, macula, and medial and posterior crista nerves. Figure 57 is a whole mount of the macula of the statocyst.

Figures 52 and 53. Perikarya in the anteroventral anterior lateral pedal lobe after filling of the brachial (figure 52) and pallial nerves (figure 53).

Figure 54. Perikarya and a few afferent fibres in the anterior lateral pedal lobe after filling of the pallial nerve. Efferent fibres are stained in the interchromatophore connective.

Figure 55. Afferent fibres in the ventral magnocellular lobe after filling of the posterior crista nerve. The fibres run in various layers but mostly centrally. (Afferent fibres of the macula and medial crista nerves show similar distributions).

Figure 56. Afferent fibres with dividing collaterals in the posterior pedal lobe after filling of the medial crista nerve. (Afferent fibres of the macula and posterior crista nerves show similar distributions).

Figure 57. Perikarya and afferent fibres in the anterior palliovisceral lobes after filling of the inferior ophthalmic nerve. Some afferents are found around the magnocellular/palliovisceral branch of the posterior superior ophthalmic nerve (posterior root).

Figure 58. Secondarily filled neurons at the macula periphery after centripetal cobalt filling of the anterior oculomotor nerve. The dark area in the middle of the macula (at right) is a remnant of the mucus layer.

Figure 59. Perikarya and afferent fibres in the anterior part of the posterior lateral pedal lobe after filling of the macula nerve.

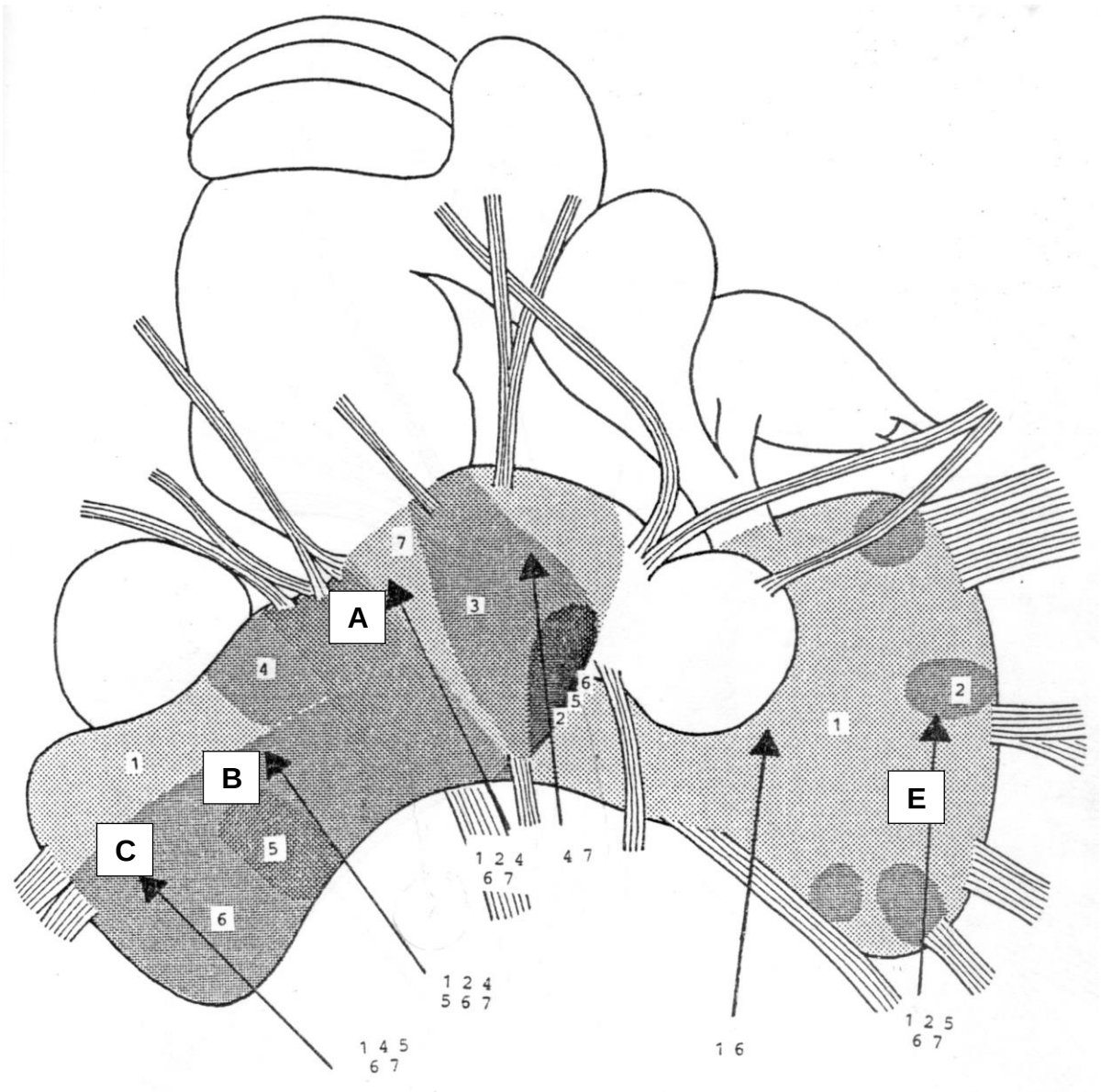

Figure 60. Semi-diagrammatic lateral view of the brain *Octopus vulgaris*, to show the regions where the efferents of the various effector systems and of the statocysts originate (stippled areas) and where their afferents terminate (arrows). The numbers indicate the following (effector) systems: arms (1), head (2), eye muscles (3,4) (4 are efferents of the posterior superior and inferior ophthalmic nerves outside the anterior lateral pedal lobe), funnel (5) (including efferents of the collar and visceral nerves), mantle (6), and statocysts (7). A-E indicate the five brain subregions A-E where afferent fibres converge (see § 4.b). For clarity, the areas of origin of the efferents (stippled areas of large diagram) are separately shown (black areas in small diagrams) for each effector system.

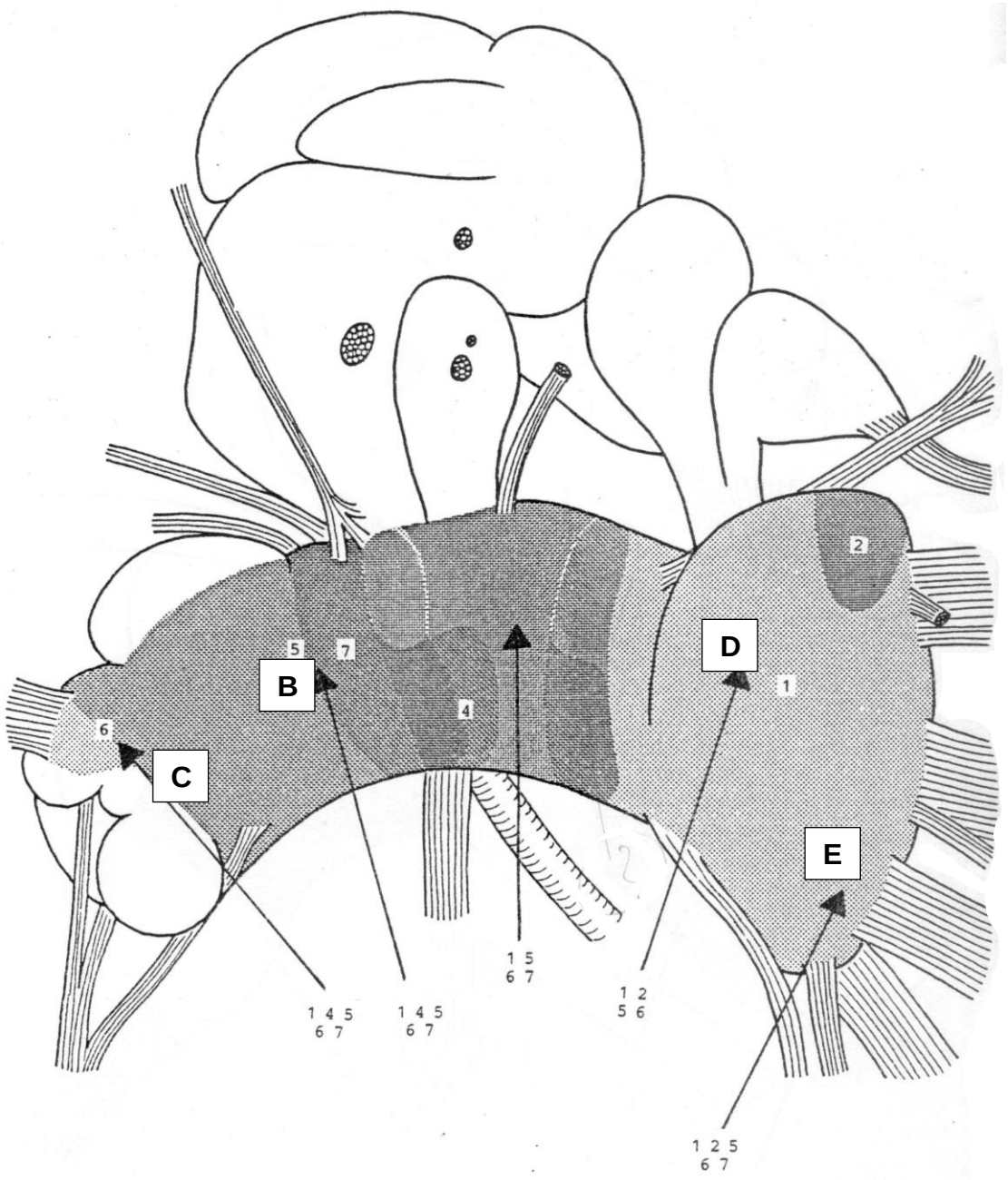

Figure 61. Semi-diagrammatic view of the brain of *Octopus vulgaris*, medial to that of figure 60. Conventions as for figure 60.

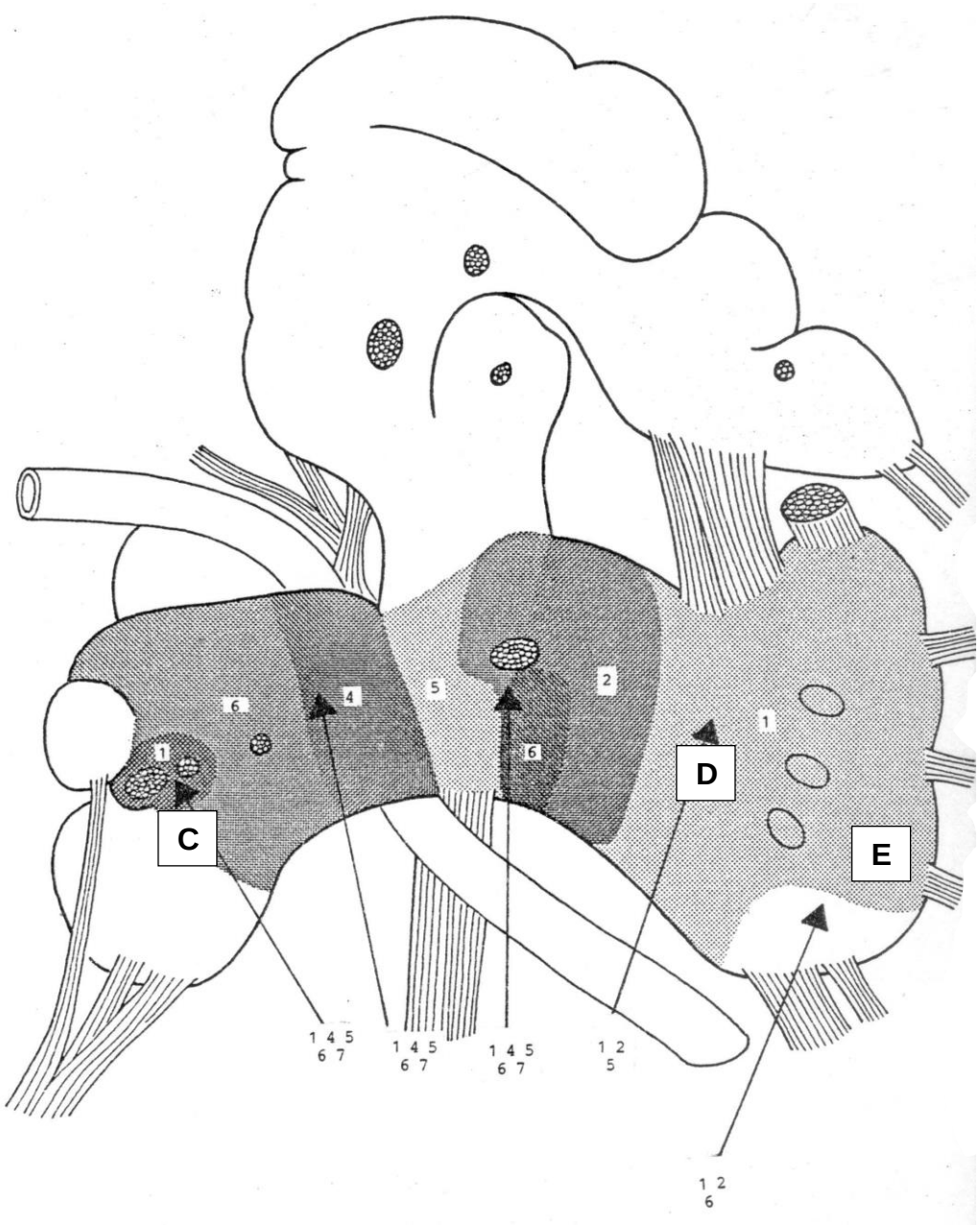

Figure 62. Semi-diagrammatic medial view of the brain of *Octopus vulgaris*. Conventions as for figure 60.

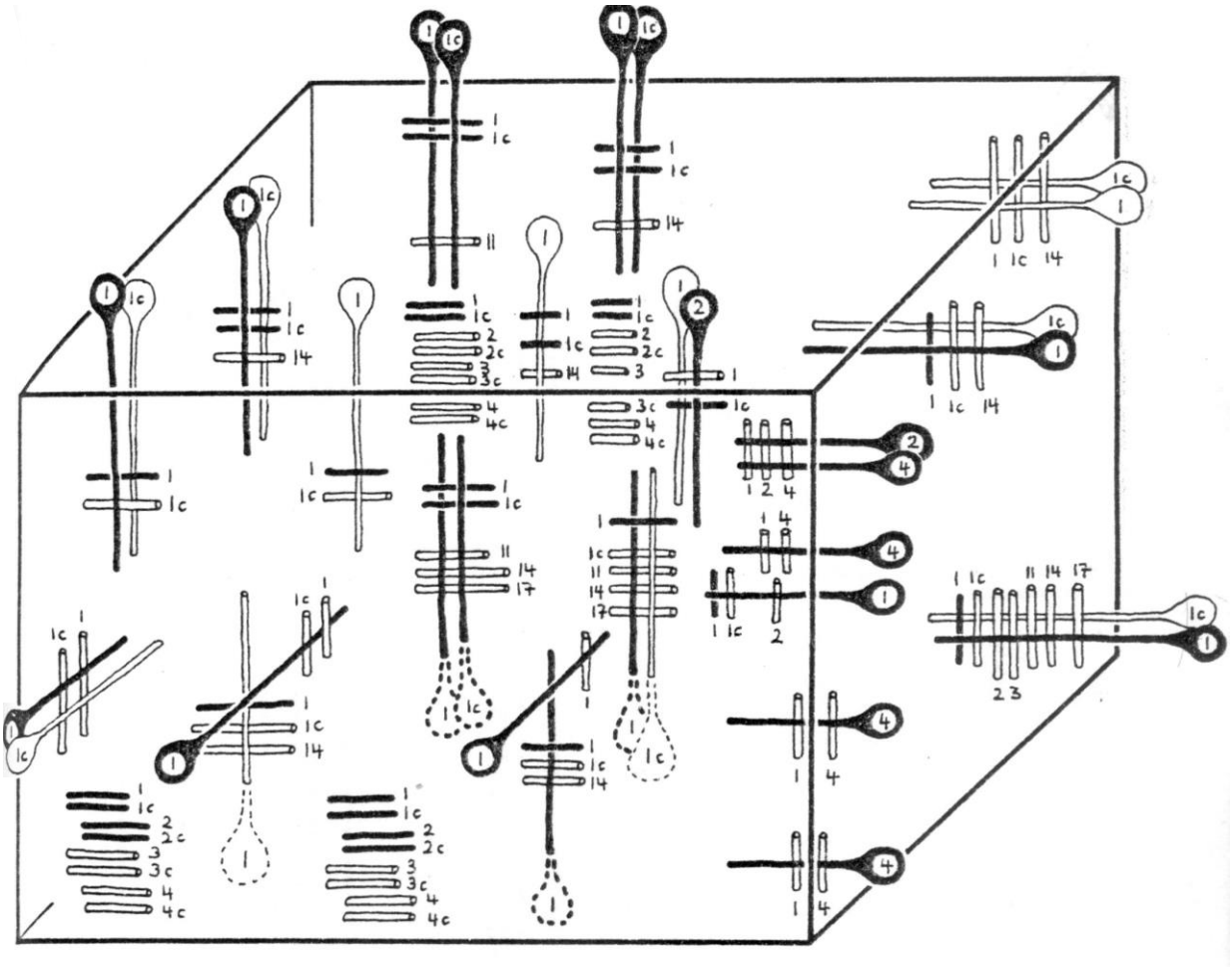

Figure 63. Diagram to show location and composition of the brain subregions in the prebrachial lobe (anterior half of diagram) and brachial lobe (posterior half of diagram) of *Octopus vulgaris* and the relative position of their afferents and efferents. Neuron symbols (with somata) stand for efferent populations and tubuli for afferent fibres. Dark symbols indicate large number of cells and fibres, light symbols of few. The numbers stand for inputs/outputs of the brachial (1), superior antorbital (2), inferior antorbital (3), interbrachial (4), head retractor (5), anterior root of posterior superior ophthalmic (6), anterior and posterior oculomotor and anterior and median superior ophthalmic (7), inferior ophthalmic (8), posterior root of posterior superior ophthalmic (9), medial pallial retractor (10), anterior funnel (11), posterior funnel (12), collar (13), pallial (14), visceral (15), macula (16), and crista (17) nerves. The symbol c indicates contralateral inputs/outputs of the relevant nerves. Within the various subregions, the spatial relation of the crossing symbols is arbitrary.

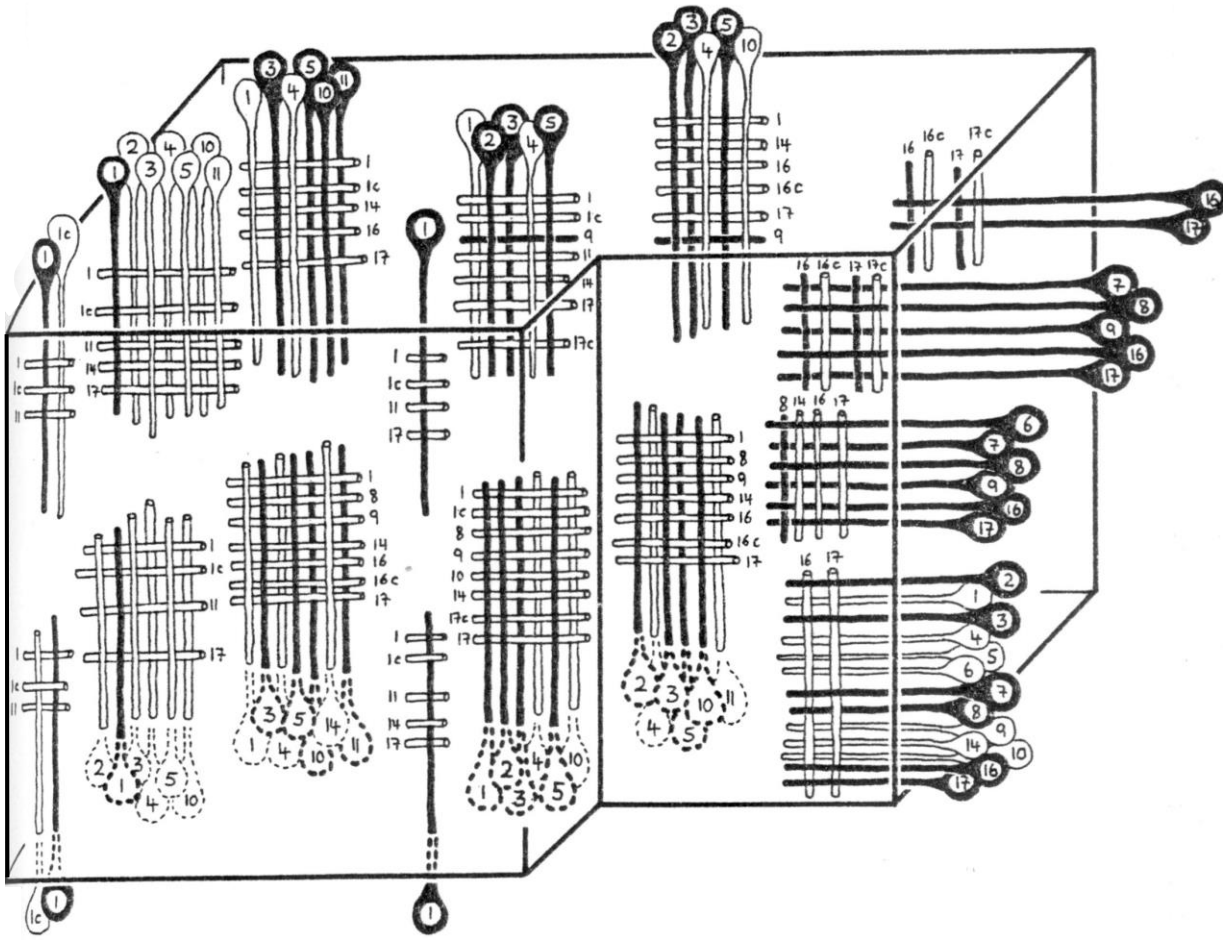

Figure 64. Diagram to show location and composition of the brain subregions in the anterior pedal lobe (left larger block of diagram), anterior lateral pedal lobe (right, smaller block of diagram) and anterior part of the posterior lateral pedal lobe (upper right corner of diagram, with two neurons and four afferent symbols) of *Octopus vulgaris*. Conventions as for figure 63.

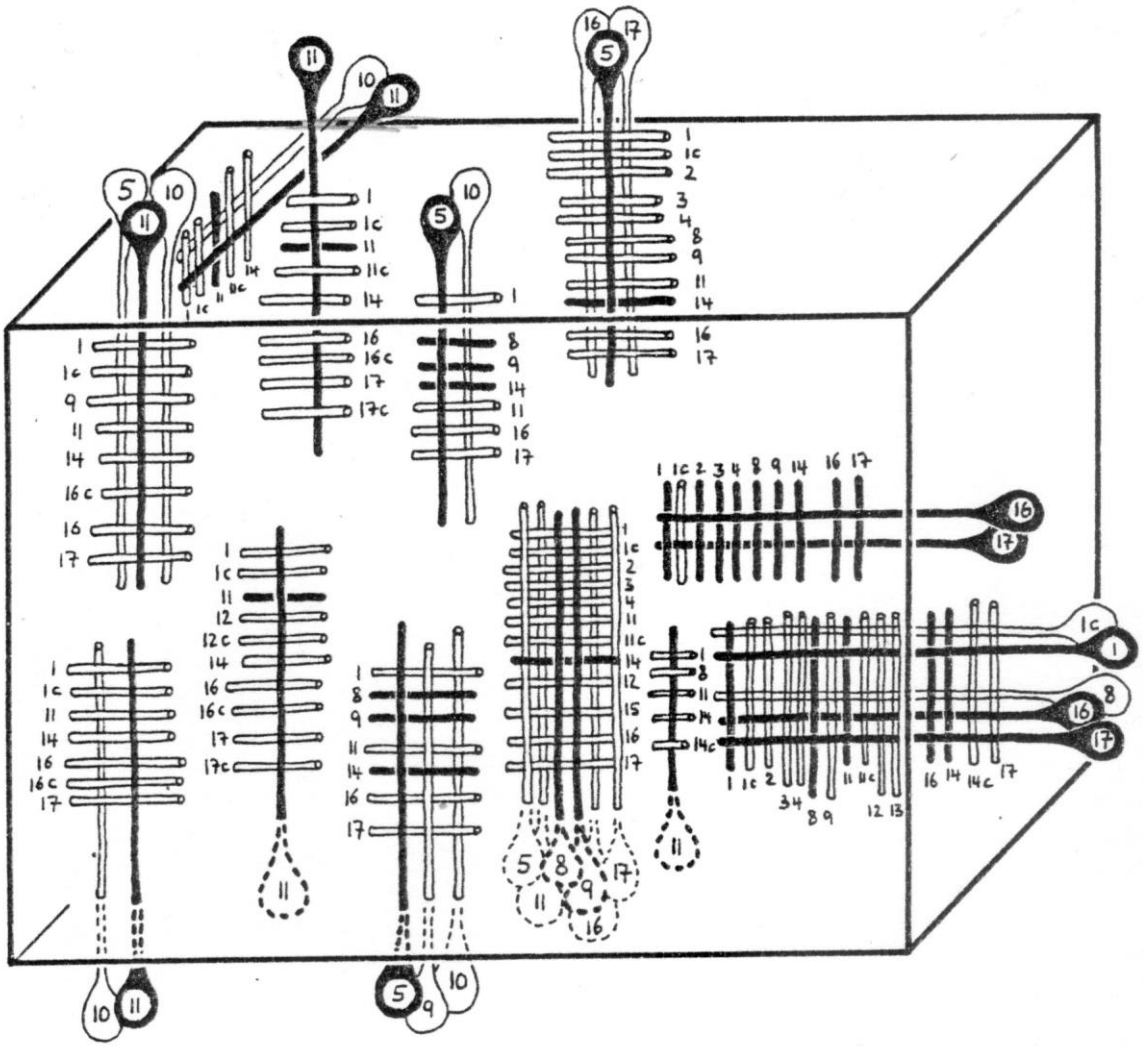

Figure 65. Diagram to show location and composition of the brain subregions in the posterior pedal lobe (left half of diagram), posterior part of the posterior lateral pedal lobe (upper right symbols of diagram) and anterior part of the ventral magnocellular lobe (lower right symbols of diagram) of *Octopus vulgaris*. Conventions as for figure 63.

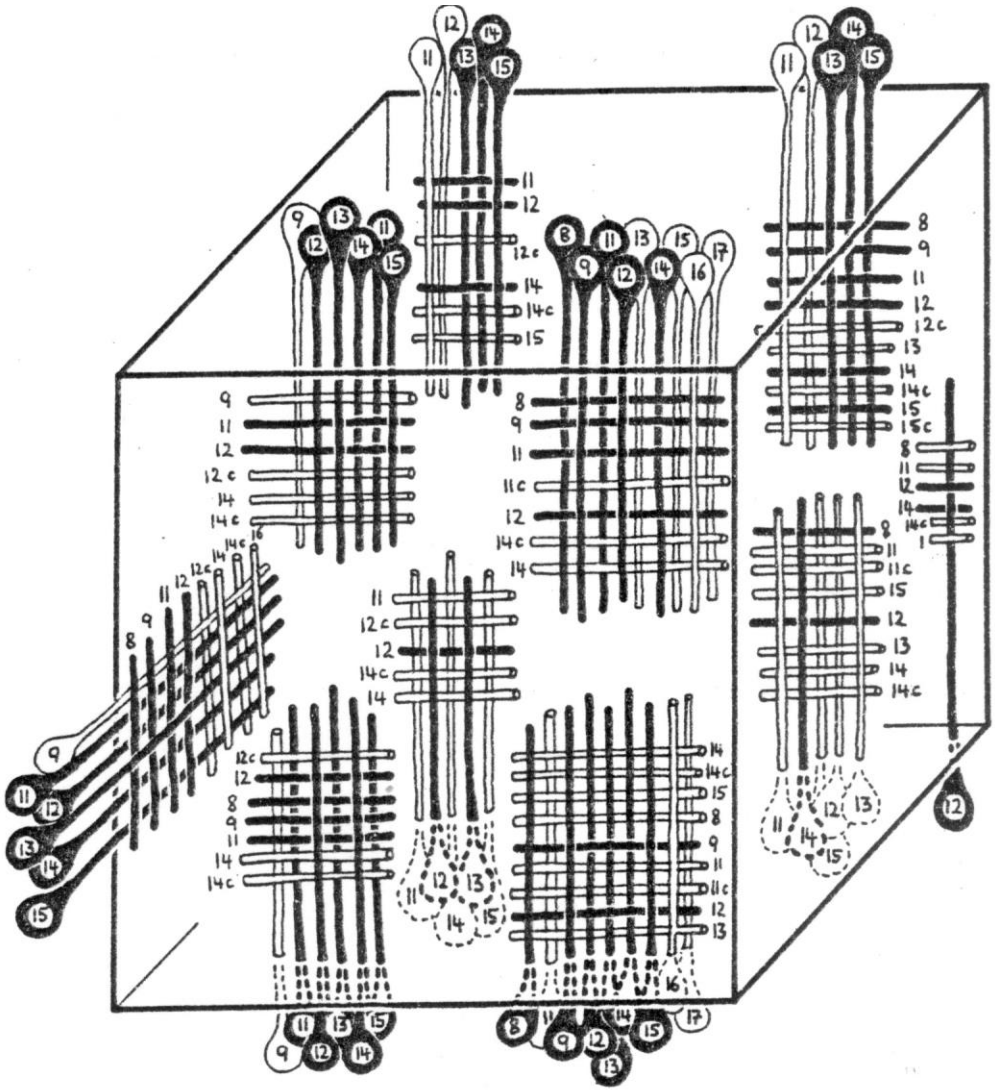

Figure 66. Diagram to show location and composition of the brain subregions in the anteriorpalliovisceral lobe of *Octopus vulgaris*. Conventions as for figure 63.

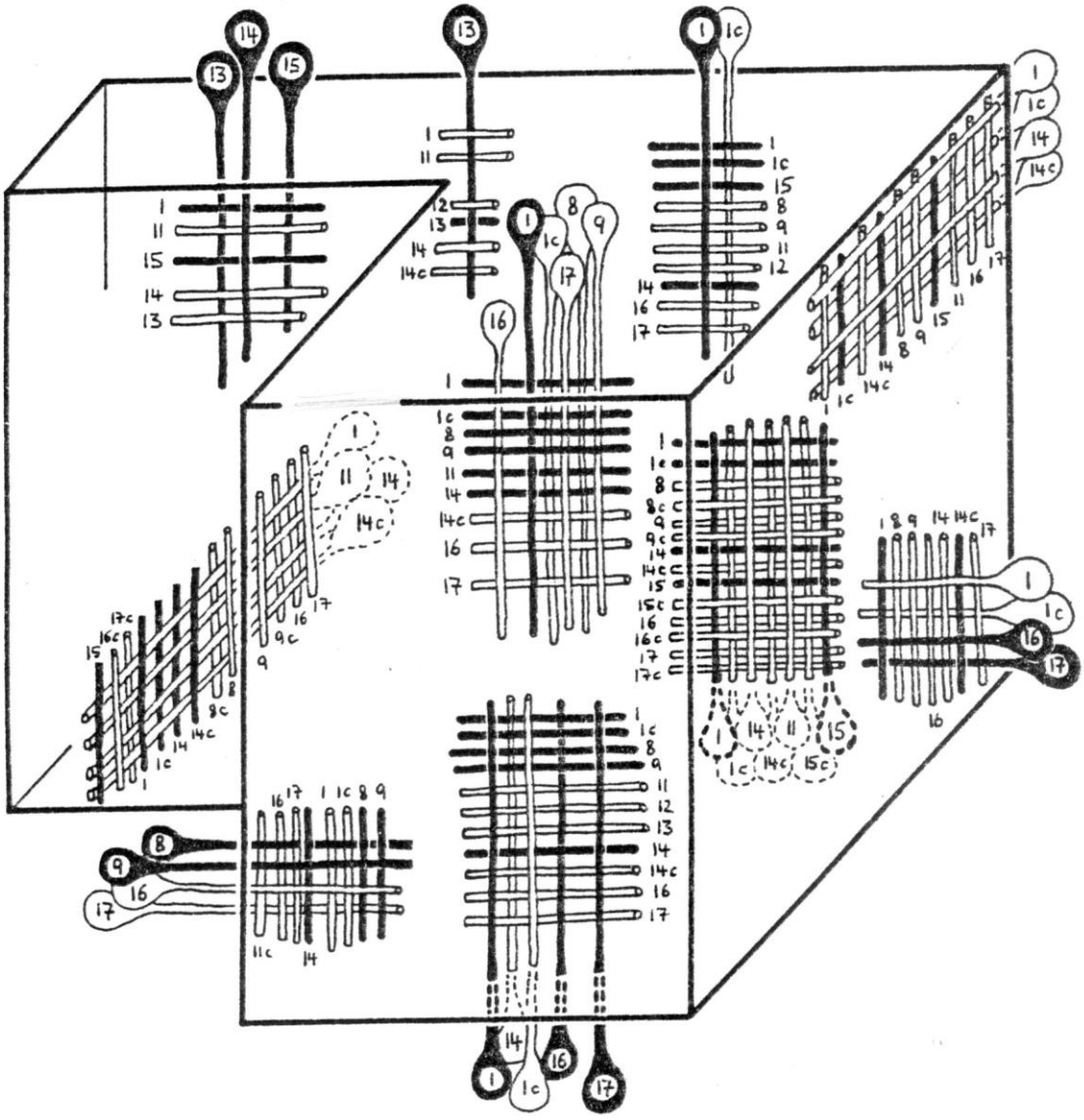

Figure 67. Diagram to show location and composition of the brain subregions in the middle ventral magnocellular (symbols in front half [to reader] of the right, larger block of the diagram) and posterior ventral magnocellular lobes (symbols in back half [away from reader] of the right, larger block and ventrally in the left, smaller block of the diagram) and in the posterior palliovisceral lobe (upper symbols in left, smaller block of the diagram) of *Octopus vulgaris*. Conventions as for figure 62.