

Light has many meanings for cephalopods

J.Z. YOUNG

Department of Experimental Psychology, University of Oxford, South Parks Road, Oxford OX1 3UD, UK

(RECEIVED August 6, 1990; ACCEPTED October 11, 1990)

Abstract

The uses of light for cephalopods living at various depths are described. Aphakic apertures are shown in the eyes of *Amphitretus* and bolitaenids. In cirrate octopods, the eye is an open cup without lens and the retinal rhabdoms are disorganized. The photosensitive vesicles of cephalopods are extraocular receptors present either in the mantle or on the head. In some mesopelagic forms, they serve to compare the downwelling light with that emitted by the animal's own photophores, thus allowing regulation of counterillumination. In bathypelagic species, the photosensitive vesicles are very large and may serve to ensure reproduction at great depths.

Some of the uses of the paired eyes in shallow water species are discussed. The mechanism for visual learning consists of a system for allowing many possible combinations of the output from numerous feature detectors. This begins with a set of columns in the optic lobes, followed by a tangential system. Outputs from the optic lobe lead to either attack or retreat: a third output leads to a memory system of four matrices allowing for interaction among the visual signals and between them and signals of taste or pain. These matrices allow conjunctive interaction between particular sets of signals and the setting up of memories ensuring appropriate responses. The matrices may be considered as analogous with those of the mammalian hippocampus. They include re-excitation among themselves and with the optic lobes. The tactile memory apparatus of the octopus has four similar lobes and also makes use of the four lobes of the visual system. These are therefore striking examples of adaptive networks allowing learned reactions by statistical selection among numerous channels. The anatomy, function, and generalizing powers of these networks emerged from Boycott's early work, whose significance for computation can now be appreciated.

Keywords: Cephalopod vision, Eyes in deep sea, Photosensitive vesicles, Memory in *Octopus*, Adaptive networks

Introduction

In this paper, I shall review various lines of work that have developed from the studies of *Octopus* vision that Brian Boycott and I made together 40 years ago. Some of the most striking recent discoveries have been about photoreception in the depths of the ocean, using organs that he and I discovered but whose function was then obscure to us.

Aphakic apertures

First, I shall describe the eyes of some octopods living at great depths, which have features that have not previously been described. Below 800–1000 m, the only light is that produced by other organisms, usually in the form of flashes. The function of the receptors is therefore to catch a few photons and discover where they came from, allowing the animal to escape from the sender or to eat or mate. Various strategies are used to meet this situation. The eyes of deep-sea animals are often very large—in *Architeuthis*, the giant squid, they are as big as car head-

lamps. But in some, as we shall see, they are small. Light is also often detected by extraocular receptors without any dioptric apparatus. Where there is little detail to be discerned, the eye itself may lack a lens and even if there is one there may also be aphakic apertures to let in light from different directions.

Amphitretus is a meso-bathypelagic octopod with tubular or telescopic eyes (Fig. 1). Sections show that the walls of the telescope are not pigmented and may serve as aphakic apertures to admit light. This is almost certainly the case in the deep-sea octopods *Japetella* and *Eledonella*. These eyes are placed far apart and are oval, with projecting ends pointing downwards, which are free of pigment (Figs. 2A and 2B). After cutting open the eye, we could show that light passes through the window at the pointed lower end, but the upper end is opaque (Fig. 2c). The retina is thickened at the end opposite to the window. It can thus receive light falling laterally through the lens, and also from the front and below through the window.

In the larvae of the cranchiidae, such as *Bathothetauma*, the eyes are on stalks and carry projections, which have been thought to be photophores. However, I could find no photogenic tissue (Young, 1970). Perhaps the projection is an aphakic aperture. The retina is curiously divided into three sections and the optic lobes are double.

Reprint requests to: J.Z. Young, The Crossroads, Brill, Buckinghamshire HP18 9TL, UK.

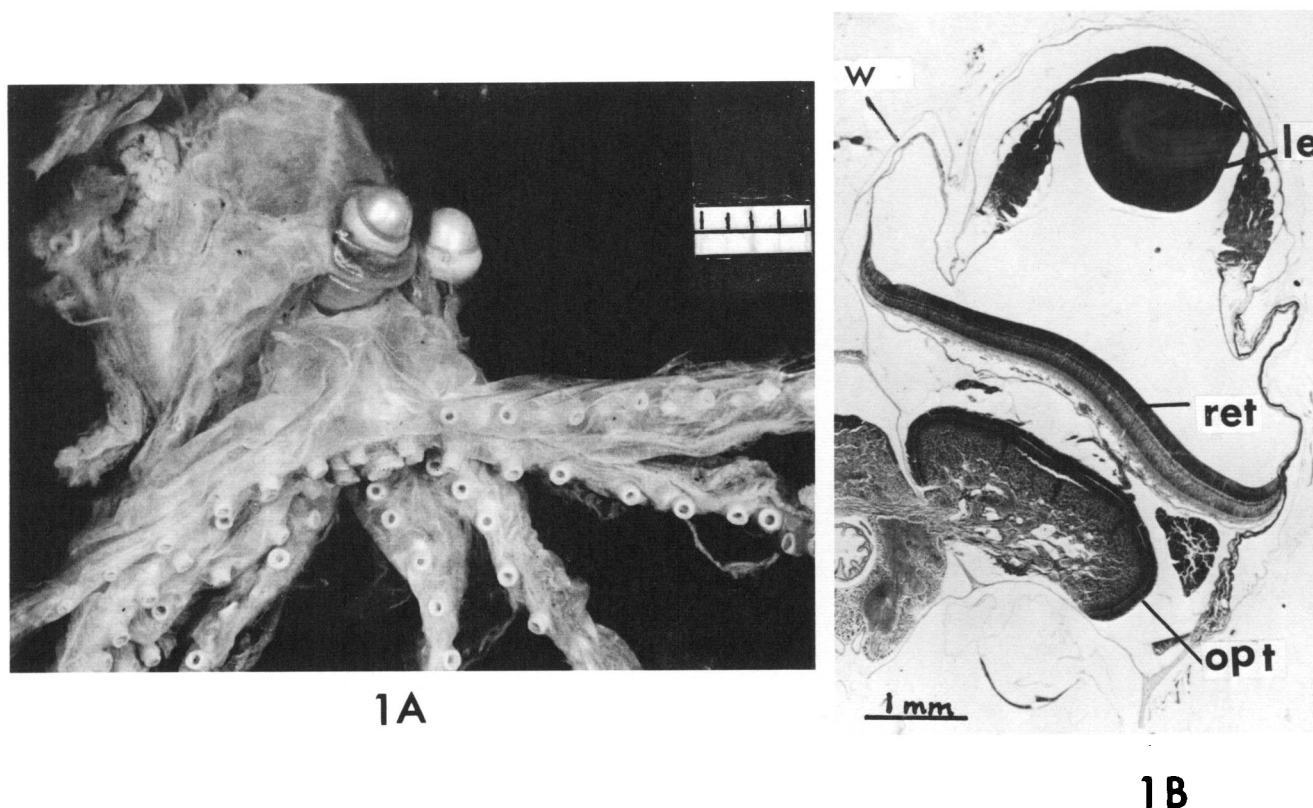


Fig. 1. *Amphitretus*. A: View of the whole animal; in life it is covered with a thick layer of jelly. B: Section of the eye showing that on one side there is an unpigmented window W; l: lens; opt: optic lobe; ret: retina; Scale bar = 1 mm.

Eyes without lenses

There is complete absence of a lens in *Cirrothauma*, one of the cirrate octopods, which live deeper than any other cephalopod, down to 8000 m in the Pacific Trenches (Aldred et al., 1983). The eye is a simple cup open to the sea, with an aperture of several millimetres (Fig. 3A). It has no sphincter and does not act as a pinhole camera, like that of *Nautilus*, but makes a good catcher of flashes presumably of prey organisms. The eyes of *Cirrothauma* again are set far apart, improving direction finding. The retina is composed of rhabdoms carrying microvilli such as those of surface-dwelling cephalopods but not collected into the regular order which, as we shall see, allows the detection of the direction of polarized light, when there is any (Figs. 3B and 3C).

Extraocular photoreceptors

For organisms living at mesopelagic depths the significance of light is more complex. Many of them make diurnal migrations, up at night to feed and down again when full of food at dawn. Measurement of light intensity may be as important as visual discrimination. Eyes with lenses are more complex than is necessary for this function and it is performed in part by extraocular photoreceptors. The discovery of these organs in cephalopods was a rather long drawn saga. The epistellar body is a small yellow spot on the hind end of the stellate ganglion of octopods. Sections showed that it was a sac with projections from the walls into the center (Fig. 8). I thought at first that it was a gland (Young, 1929).

Boycott and I found similar sacs near the olfactory lobe of

Loligo and *Sepia*, and we called them parolfactory vesicles (Fig. 4) (Boycott & Young, 1955). They were also seen and described as glands by Thore (1939) and Haefelfinger (1954). None of us suspected their true function. It was not until 1962 that Howard Bern and his colleagues showed that the projections to the center of the sacs are covered with microvilli and that these organs are photoreceptors, containing rhodopsin, but with no dioptric apparatus (Nishioka et al., 1962, 1966). Responses of the vesicles to changes of illumination were then shown by Mauro and his colleagues (Mauro & Baumann, 1968).

These organs are now called photosensitive vesicles and they have been fully described and their function discussed in the extensive studies of R.E. Young (1977, 1978) in Hawaii. In squids living in midwater (350–750 m), the vesicles serve to regulate the light emitted by the animal's own photophores to provide protection from predators by counterillumination. To be effective, this emitted light must match the downwelling light over a range of wavelengths, intensity, and direction. In these squids, there are dorsal photosensitive vesicles to detect the light from above and ventral ones to measure that from the animal's own photophores (Fig. 4 and 5). The nerves meet in the peduncle lobe, which must serve to regulate the output. Young et al. (1979) were able to prove this function experimentally. It is interesting to note the simplicity of the neural apparatus that makes these comparisons (Fig. 5), in contrast with the complexity of the optic lobes serving for vision as we ordinarily think of it (p. 6). The control of the output of the photophores is probably through the subpedunculate lobes, which are adjacent to the peduncle lobes and are large in other cephalopods with elaborate control of luminescence (Nixon & Young, unpublished).

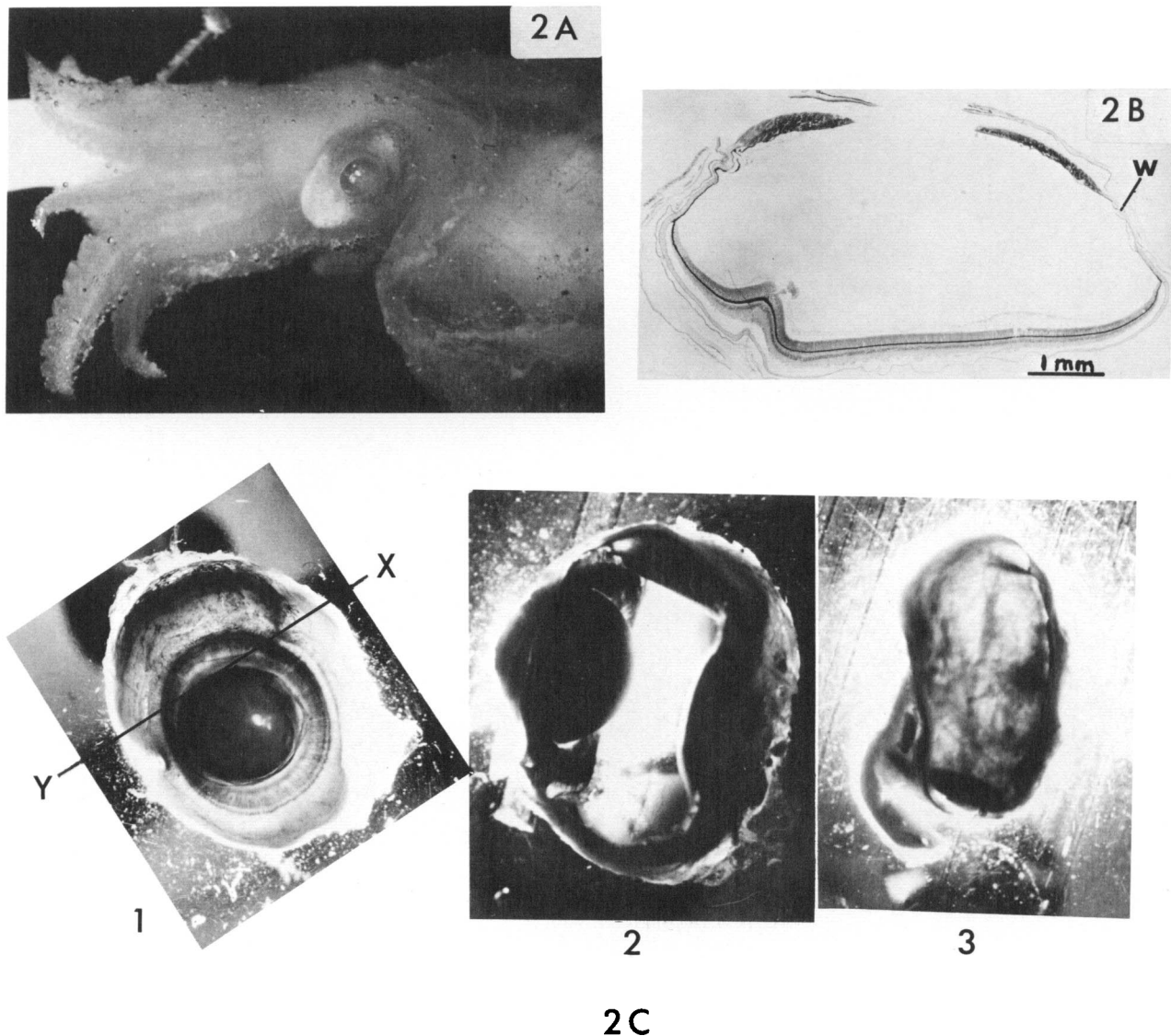


Fig. 2. *Eledonella*. A: View of L eye. B: Section of eye after removal of the lens. The lower end (to the right) is an unpigmented window W. The retina is thickened at the upper end (the bulge in it is an artefact). C: 1—shows the whole eye and the line of cut is at XY; 2—shows the lower end with a light behind it shining through the window; and 3—shows the upper end with a light behind it blocked by the pigment.

At depths greater than 750 m, no counterillumination is needed but the photosensitive vesicles are present as very large sacs on either side of the brain (Fig. 6). They are packed with rhabdoms bearing microvilli and often quite irregularly arranged (Fig. 7). There is still speculation about their function at these depths: it is almost certainly related to reproduction. The peduncle lobe, where their nerves enter, lies close to the lobe that innervates the optic gland (Fig. 5). Surgical interference in this region leads to premature ripening of the gonads in *Octopus* (Wells, 1978). Moreover, the onset of reproduction is induced by darkness in *Sepia* (Wells, 1978). In species that breed near the surface, the photosensitive vesicles may be part of this mechanism that ensures breeding in the spring. In the species that breed at very great depths, the vesicles must provide sensitivity to very low levels of illumination. Presumably they serve to keep the squids from maturing until they are very far down and then to hold them there, out of danger from predators

while they breed. However, no precise correlation between depths of egg laying and size of photosensitive vesicles can yet be drawn.

The epistellar body is especially interesting in octopods that live at great depths. Here there is no evidence that it is concerned with reproduction, but it is always larger in deep-sea animals than is the small epistellar body seen in *Octopus*. For instance in cirrate octopods, the epistellar bodies are quite large and the structure of the rhabdoms can easily be seen (Fig. 8). A possible function of these large photoreceptors is to give signals to clear the transparent mantle of luminous organisms, which would make the animal conspicuous to predators. This provides a hint that in *Octopus* itself the epistellar body may function in that way while the larvae are pelagic. There is some evidence that in the adult octopus it is degenerate; the cavity often contains amoebocytes, indeed these were already seen in 1929.

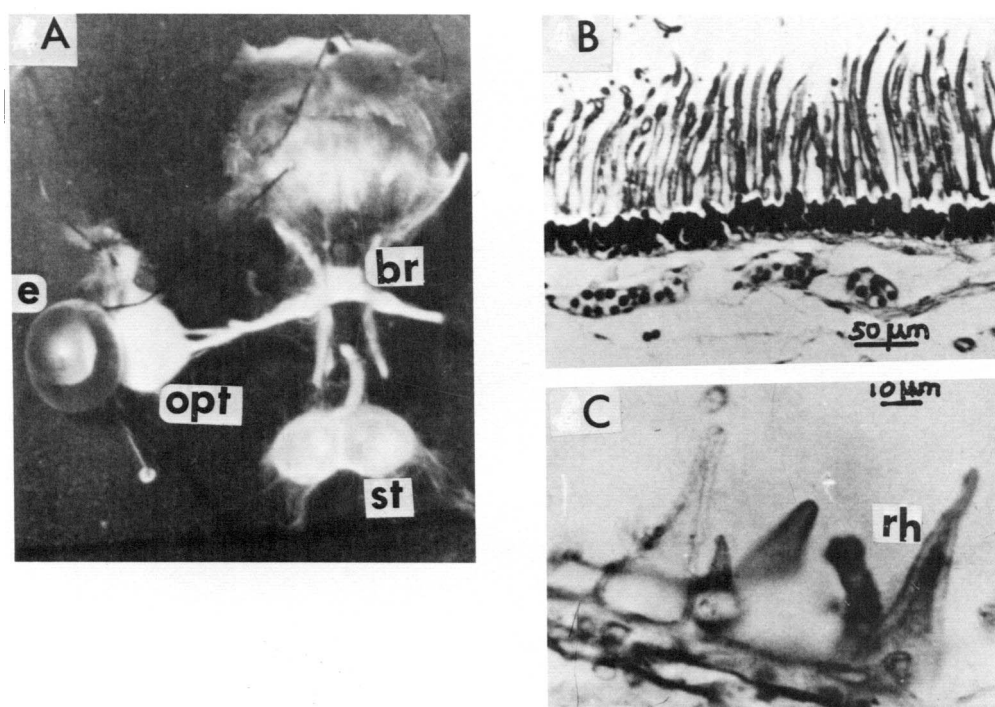


Fig. 3. *Cirrothauma*. A: Dissected specimen. e: view of open eye on left; opt: optic lobe; br: small brain; and st: large statocyst. B: Section of the retina, showing irregular rhabdoms. C: Part of the retina at higher magnification, showing the isolated rhabdoms, rh.

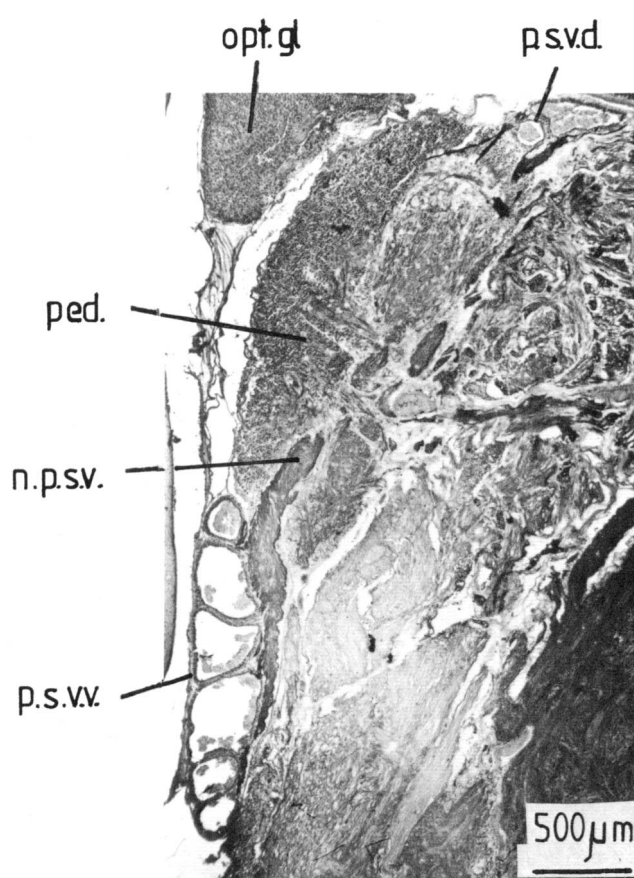


Fig. 4. Transverse section of the photosensitive vesicles of the midwater squid *Illex*. Cajal silver stain. n.p.s.v.: nerve of the ventral vesicles; opt. gl: optic gland; p.s.v.d.: dorsal photosensitive vesicles; p.s.v.v.: ventral photosensitive vesicles; and ped.: peduncle lobe.

Vision and patterns of behavior

It is time to return to the various uses of the true eyes. They are usually larger in mesopelagic squids than in those at the surface, presumably to catch more light. The optic lobes are also very large and well-differentiated. In species living in shallow waters, the eyes have many functions. They are of course involved in the recognition and capture of prey and the avoidance of enemies. They provide the information that allows for the production of elaborate color patterns for concealment. However, there is no convincing evidence for color vision in any cephalopod, although three visual pigments are reported in the squid *Watasenia* (Seidu et al., 1990).

Vision also plays a large part in intraspecific reactions such as shoaling and also in elaborate courtship displays. These may involve remarkable patterns and strange postures of the arms and papillae on the skin (Hanlon & Messenger, 1988). The use of these elaborate systems of signalling must involve correspondingly complex powers of visual analysis to interpret them. Presumably there is little of this complex behavior at greater depths, where the animals seem to maintain a more uniform color, but of course they have been little studied. In a few species of squids, photophores differ in the two sexes and light is presumably used to find a mate. Thus, in many cranchiids the mature females have luminous organs on the tips of the arms. The adult male *Ctenopteryx* emits light of a very short wavelength such as is not detected by the eyes of most fishes and may thus be a safe signal to send for successful sex.

Discrimination of polarized light

The arrangements in the retina of *Octopus* allow for discrimination of the direction of polarization of light. This capacity is

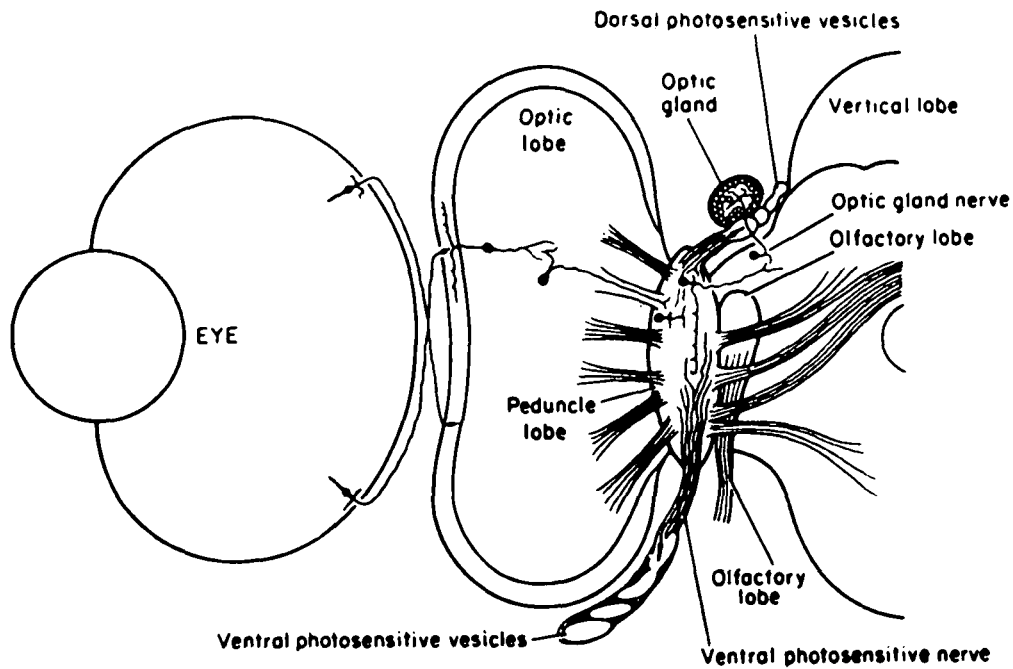


Fig. 5. Diagram of the connections of the photosensitive vesicles in a mesopelagic squid.

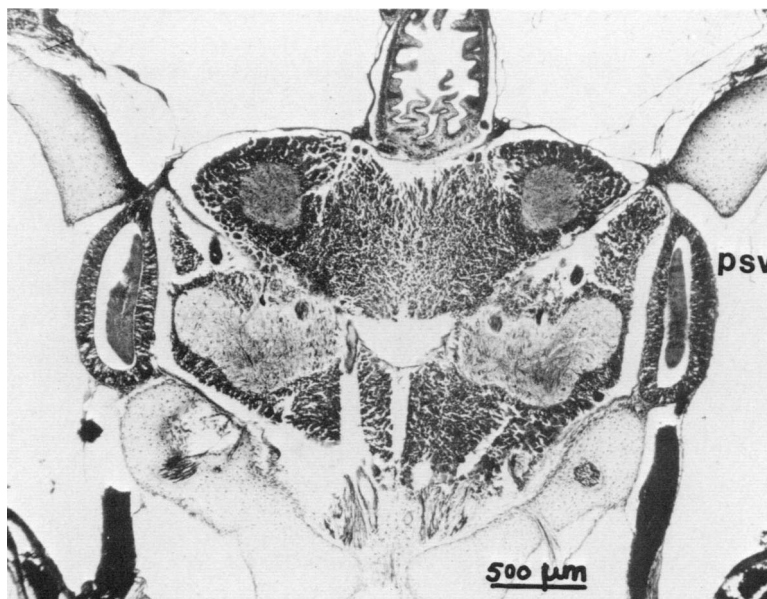


Fig. 6. Transverse section of the cranchiid squid *Teuthowenia* to show the large photosensitive vesicles, psv, at the sides of the brain. Cajal silver stain.

probably present in other cephalopods, at least in those living near the surface. The microvilli of the rhabdoms carrying the chromophore lie on opposite sides of a central axis and the units are arranged in pairs. This provides the capacity for the detection of the plane of polarized light, which was first shown to occur in *Octopus* in behavioral experiments by Moody and Parriss (1961) and confirmed by Saidel et al. (1983). It remains uncertain what use is made of this facility, but in shallow water there must be many differences in the planes of polarization of reflected light.

Visual discrimination and learning

The retina of an octopus contains 120 million rhabdoms and the optic lobes 60 million cells. This large equipment allows the elaborate visual discrimination that is characteristic of much of the cephalopod behavior. Little is known about the extent of in-born visual capacities. Newly hatched *Sepia* at once attack mysid shrimps, but in subsequent days they learn to discriminate them better from irrelevant objects (Wells, 1962). In general, animals must learn to categorize objects and events around

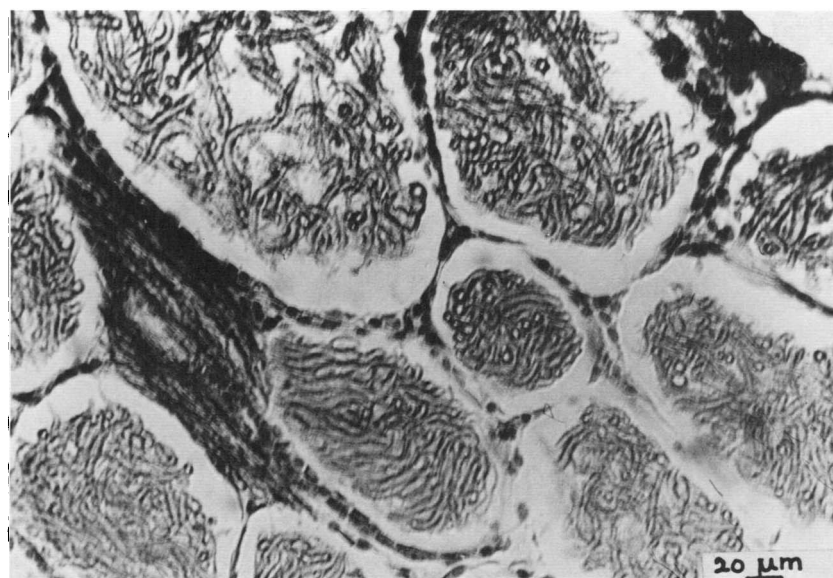


Fig. 7. Section of the photosensitive vesicles of the bathypelagic squid (*Bathyteuthis*). Each sac is filled with rhabdoms, irregularly arranged and often twisted. A bundle of nerve fibers is seen. Cajal silver stain.

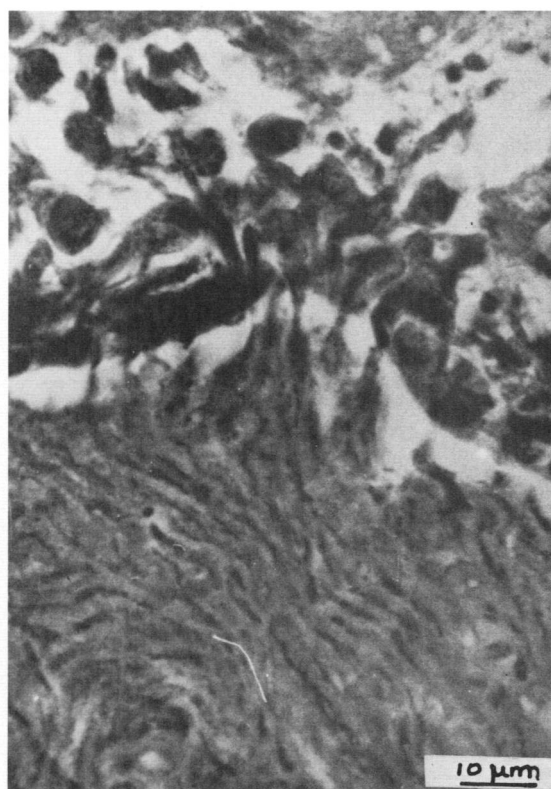


Fig. 8. Section of the epistellar body of the cirrate octopus (*Stauroteuthis*). The long irregular rhabdoms can be seen attached to their cell bodies in the wall of the vesicle. Cajal silver stain.

them and octopuses are certainly able to do so, as Boycott and I were soon able to show experimentally in 1950 (Young, 1961). Later, we described the brain pathways and lobes that are involved and showed the effects of removing them on the process

of visual learning. We could not fully interpret our findings at the time, but it is now very interesting to reconsider the possible functions of the circuits that are involved, in the light of recent views on the functioning of adaptive networks in mammals (see Kohonen, 1988; Rolls, 1990).

The principle is to maximize the possibility of forming conjunctions between groups of inputs from feature detectors, combining them with signals of evaluation of reward or trauma and recirculating the particular combinations so that their effects are reinforced (Fig. 9). The essence of the system is the multiplicity of the channels and the statistical possibilities of interaction that they offer. Anatomical study reveals these patterns of connections, which cannot yet readily be investigated in any other way. It is useful therefore to reexamine the evidence of their memory functions, making reasonable assumptions about changes in synaptic efficiency.

Visual feature detectors

The axons of the retinal cells pass through an elaborate chiasma, which projects the reinverted pattern on to the optic lobe, as was shown long ago in an excellent study of *Sepia* by Cajal (1917). This retention of topology in the projection is itself of great interest. In the optic lobe, the fibers end in contact with a remarkable set of dendrites lying tangentially in the plexiform zone (Fig. 10). These run in many directions, some for long distances. In some layers of the plexus they are mainly at right angles to each other and set in the main planes of the animal. It seems likely that these second-order visual cells serve as feature detectors, stimulated by the contours in a scene. It was indeed shown that octopuses distinguish vertical and horizontal figures more readily than those at other angles (Sutherland, 1958). However, it is the great *variety* of the directions and lengths of these dendrites that provides the possibility of recognition of the many shapes and scenes that an octopus meets as it finds a home and forages around for food and avoids its enemies.

The question is how does the system combine particular sets or conjunctions of inputs from these and other feature detec-

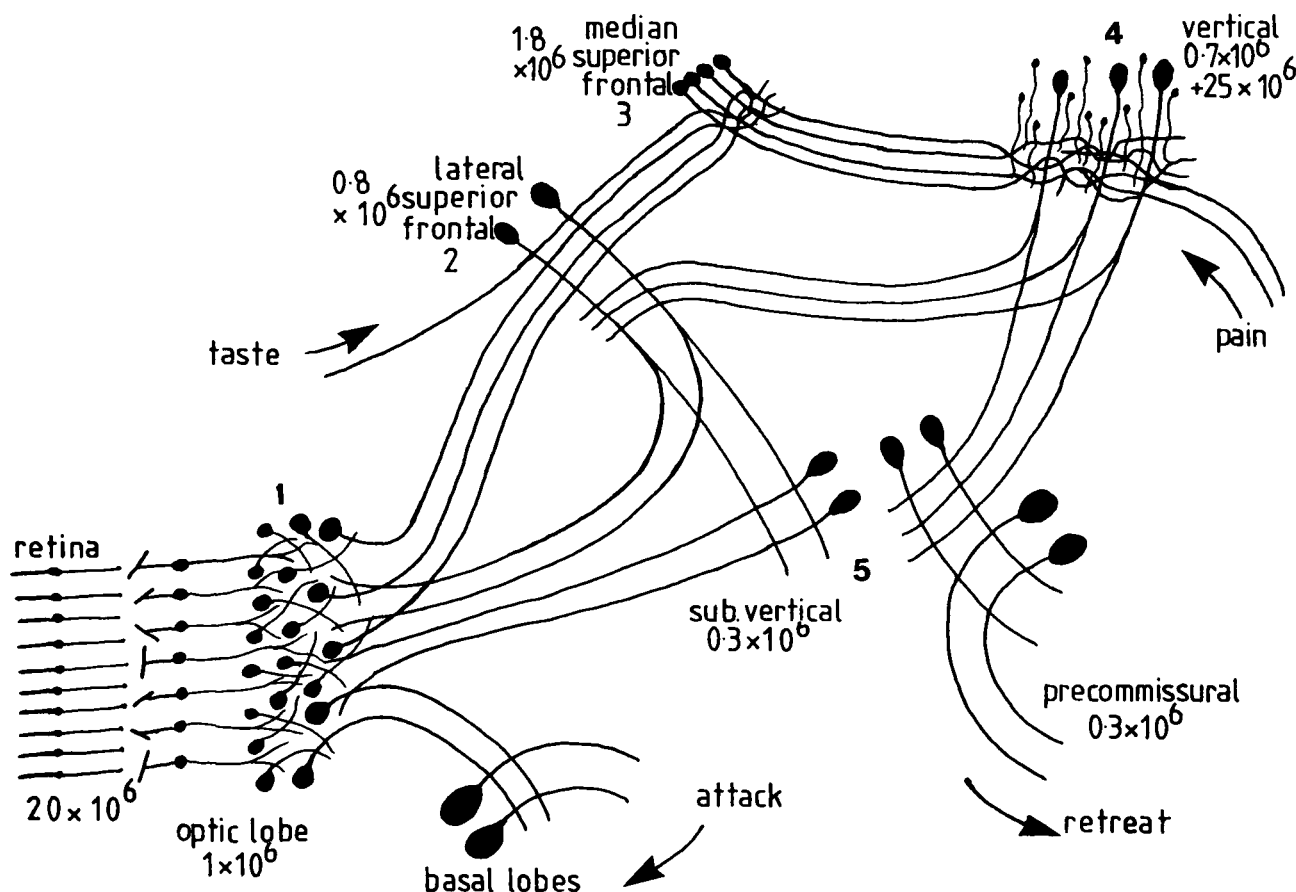


Fig. 9. Diagram of the matrix connections in the visual memory system of *Octopus*. The successive matrices are labeled 1–5 and the number of cells in each lobe is given.

tors and make a record that ensures appropriate behavior if similar events recur? The axons of these second-order visual cells form a system of columns with progressively wider interactions passing centrally (Fig. 11). Unfortunately, the precise connections within and between the columns are not known and are shown only schematically in Fig. 9. They would be worth further close study. It is surely significant that such columns occur in the system concerned with visual discrimination, as they do also in insects and in mammals. It seems certain that these columns and networks provide the first stages of the formation of conjunctions between sets of visual inputs. The second and/or third order visual neurons then pass on signals either to motor centers, or to the highest cerebral centers, which Boycott and I showed to be concerned with learning (see Young, 1965, 1971).

There are three relevant output pathways from the optic lobes (Saidel, 1982) (Fig. 9). One passes directly to the escape mechanisms of the magnocellular lobe and this is probably used for avoidance when large objects threaten, perhaps those that stimulate the largest feature detectors. This pathway is not shown in Fig. 9. A second pathway leads to the peduncle lobe and basal lobe system, which directs precise movement, including probably attack, as Boycott showed in *Sepia* (Boycott, 1961). This is presumably the pathway for attack in situations that have become familiar by use of the learning mechanisms.

The third pathway leads to the vertical lobe system, and this is responsible for learned visual behavior. It consists of a series of four lobes in which the visual signals pass through matrices

with re-entry, allowing them to form conjunctions. Interaction with signals of taste and of trauma provides for decision as to appropriate action. Modification of synapses provides the necessary memory record, distributed throughout the system.

In the first of the four lobes—the lateral superior frontal—the fibers from the optic lobes cross the dendrites of the cells of the lobe, forming a typical lattice-like matrix (Fig. 12). Here also fibers enter from the lips, allowing combinations of particular patterns of visual input with signals of taste. This lateral superior frontal lobe also receives recurrent fibers from the vertical lobe and is thus subject to re-excitation. The output fibers from this lobe go partly back to the optic lobe and partly to the fourth lobe—subvertical—which also sends signals to the optic lobe. This re-excitation is fundamental for the attack system: after injury to the lateral superior frontal lobe an octopus no longer makes any attacks at distant objects, although it is not “blind” and will put out an arm to take a crab nearby.

The second of the lobes—the median superior frontal—receives all of its input by visual and taste fibers that have passed through the first lobe (Fig. 12). In this second lobe, the visual and taste fibers interweave in a complex plexus. This allows maximum possibility for each of the output cells of the lobe to be stimulated by a particular combination of the visual and taste inputs. All of the output fibers of this lobe pass on to the third matrix, in the vertical lobe. Here they make synapse with relatively few large cells carrying numerous dendrites, which are thus well-suited to receive multiple inputs (Fig. 13). Another set of fibers enters the vertical lobe from below and is presumed to

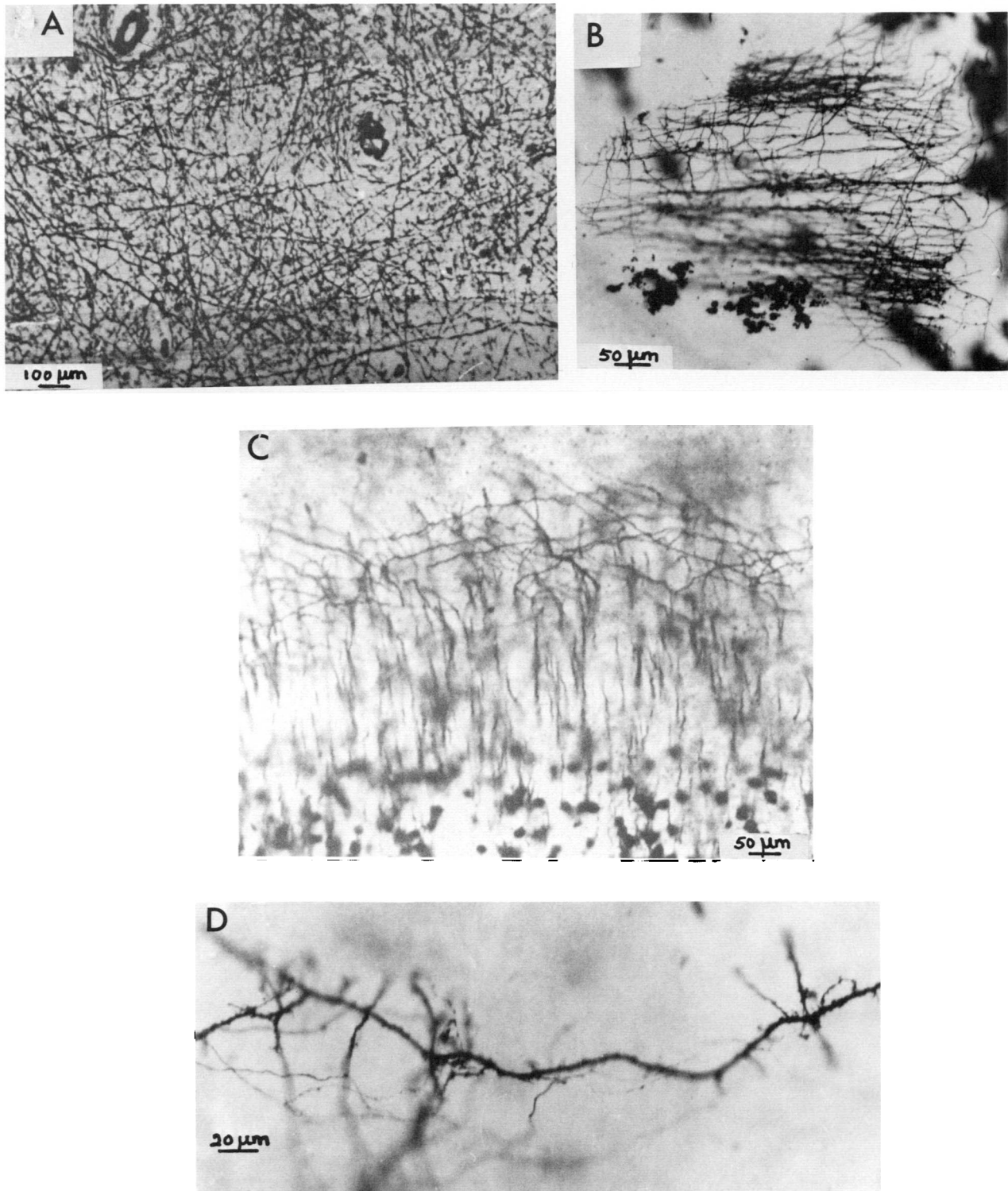


Fig. 10. Sections tangential to the surface of the optic lobes to show the oriented dendrites in the plexiform layer. Golgi stain. A, C are from *Loligo*, and B, D from *Alloteuthis*. D: Collateral twigs on a single trunk.

contain fibers signalling trauma. Boycott and I showed many years ago (1950) that after removal of the vertical lobe an octopus shows lack of restraint. It will continue to make many attacks at a crab under conditions from which it receives a shock. It can retain a memory not to do so only for a very few minutes. In addition to its large cells, this lobe contains 25 million minute amacrine cells, whose axons do not leave the lobe. The

precise connections are still uncertain but one possible version is shown in Fig. 14. The amacrine cells are presumably involved in the establishment of specific connections of the larger cells to constitute a memory record that prevents attack in a particular situation.

The output fibers from the vertical lobe pass to two targets—partly back to the first matrix, in the lateral superior

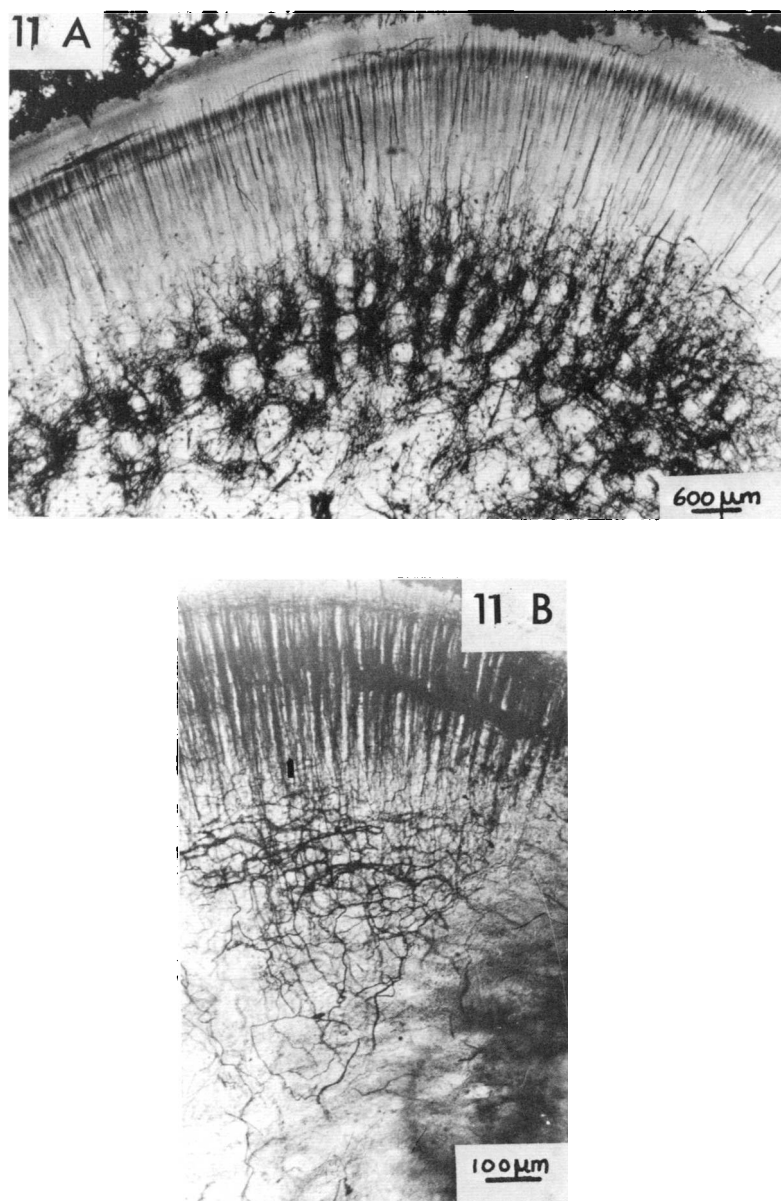


Fig. 11. Sections of the optic lobe to show the columns formed by the axons of the second-order visual cells and the tangential connections made at the center of the lobe. Notice the larger radial fibers towards the hilum in part B. Both sections are of *Loligo*. Golgi stain.

frontal and partly down to the subvertical lobe. This last is the fourth lobe of the circuit and has rather few large cells. It sends its axons partly back to the optic lobe, completing the major circuit, while other fibers pass down to the precommissural lobe, whose large fibers run to the magnocellular lobe, which produces actions of retreat.

This system allows for learning either to attack when one particular combination of visual features is associated with a food reward, or to retreat from it if there is trauma. The initial response of an octopus to an unfamiliar visual situation is a delayed slow attack. The signals for this presumably pass from the optic lobe to the basal lobe motor pathway and *also* around the vertical lobe circuit. If food results, this combination is reinforced along the circuit through the lateral superior frontal back to the optic lobe and again through the circuit from the vertical to lateral superior frontal and yet again round

the whole loop from the subvertical back to the optic lobe. All of the relevant synapses in all these lobes may be facilitated and a memory ensuring attack in this situation will be spread among all of them.

If, however, the particular visual combination results in pain the circuit through the vertical lobe now produces retreat. The synapses are changed so that this combination of input signals no longer tends to produce attack. The re-excitation circuits through the superior frontal lobes and optic lobes serve to maintain this condition and establish a memory record.

Brian Boycott and I made studies of the effects of injury to various parts of these circuits (see Young, 1964, 1965; Wells, 1978). After removal of the vertical lobe, it is difficult to train an octopus not to make attacks at its familiar prey, such as crabs. Normal octopuses that have received a 12-V shock will not attack again for several hours, but in those without verti-

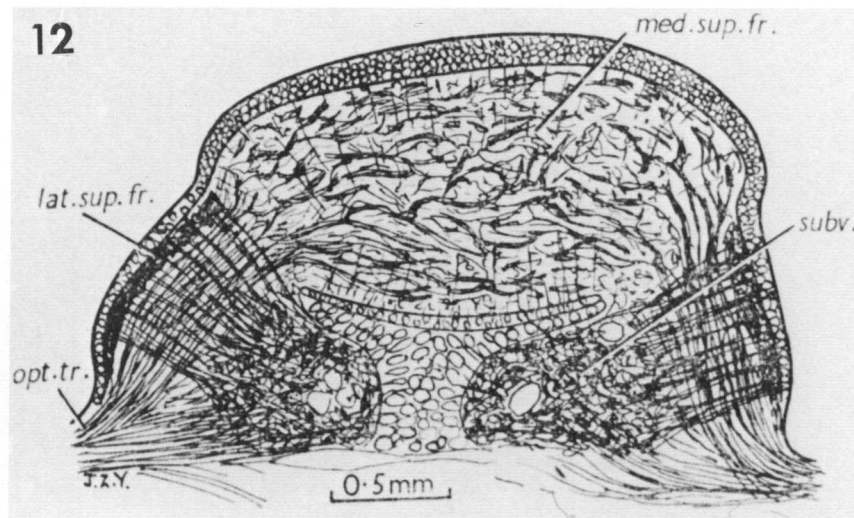


Fig. 12. Drawing of transverse section of the lateral and medial superior frontal lobes of *Octopus*. Notice the regular matrix in the lateral lobe (lat. sup. fr.) with axons passing to the subvertical lobe (subv.). In the median superior frontal lobe (med. sup. fr.), the afferent fibers from the optic tract (opt. tr.) interweave as they cross the trunks and dendrites of the cells of the lobe.

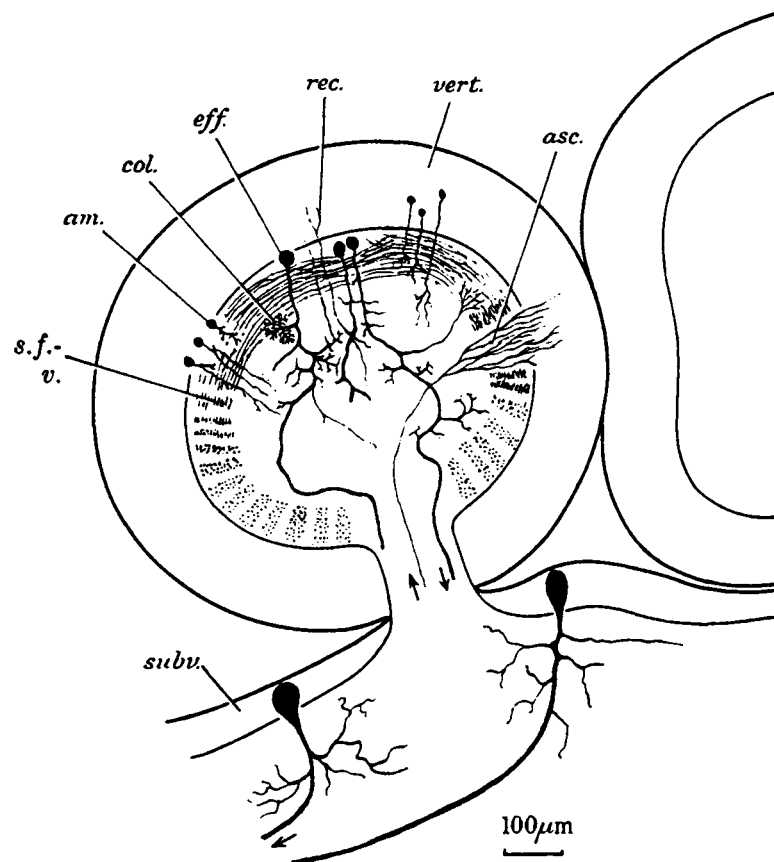


Fig. 13. Transverse section of one of the vertical lobes of an octopus (vert.) showing around the edge the incoming bundles of the superior frontal to vertical tract (s.f.-v.). Some of these fibers are seen running tangentially in the outer part of the neuropil. Here they cross the main trunks of the efferent cells of the lobe (eff.) and the amacrine cells (am.). The efferent trunks show bushy collaterals (col.) and recurrent branches reaching the cell layer (rec.). The ascending (?pain) fibers (asc.) branch in the outer neuropil, the twigs reaching to the cell layers. Two of the large subvertical cells with axons proceeding to the optic lobes are shown (subv.). Figure combined from drawings of Golgi preparations but only approximately to scale.

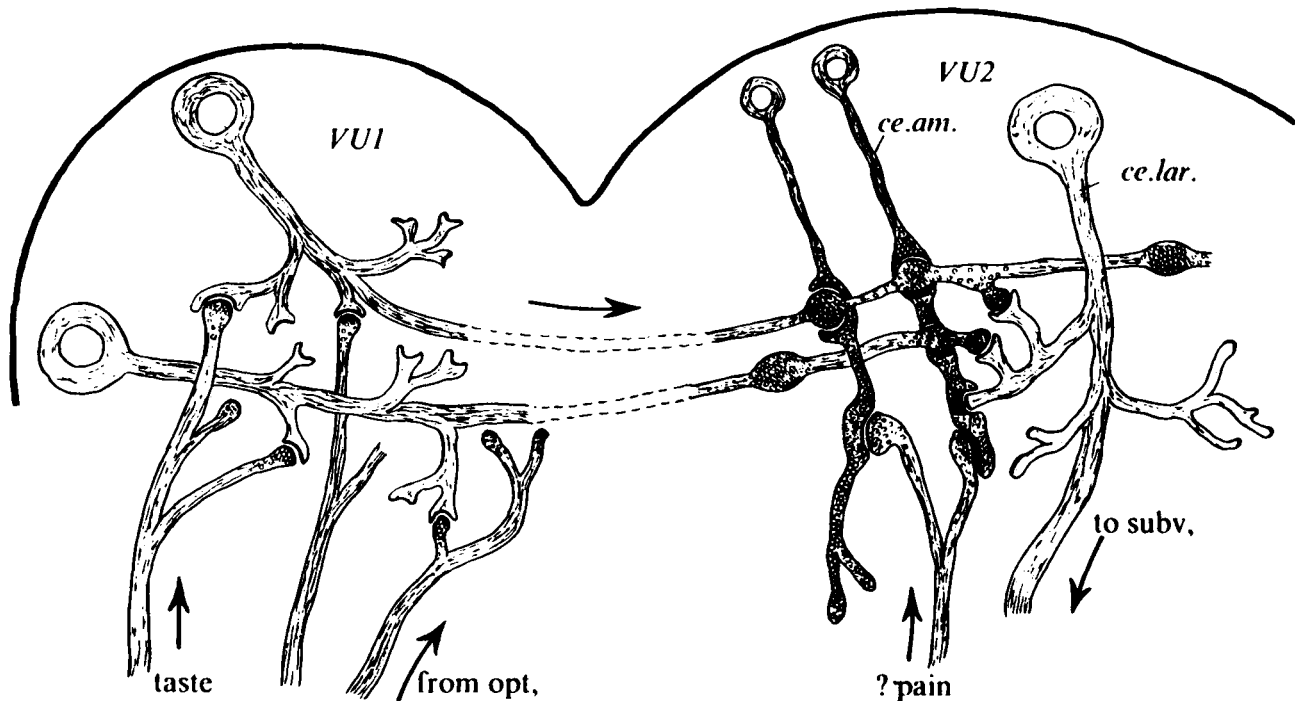


Fig. 14. Diagrammatic reconstruction of possible connection patterns of the median super frontal (VU1) and vertical lobes (VU2) from the electron-microscopic studies of Gray and Young (1964). The connections of the pain fibres are uncertain and they may make synapse with the large cells (ce.lar.) as well as with the amacrine (ce.am.).

cal lobes there is restraint only for a few minutes after a shock, whose effect quickly passes off. If, however, after a shock a crab is left in view of the octopus, or is shown at intervals of say three minutes, then the inhibition can be maintained for a while. Evidently, the vertical lobe with its small cells is responsible for maintaining some inhibitory state that is set up by a shock. After partial removals, the accuracy of response was proportionally reduced.

The functions of these matrices of course depend upon their synapses. We lack information about transmitters, modulators, second messengers, and internal synaptic metabolism. This is badly needed, but already from study of the organization we begin to see how this complex system may operate in the life of an octopus. The matrices allow for estimates of the probable nature and effects of situations, even if they recur never quite the same, but in varying combinations. Such a capacity for *generalization* is an essential requirement for complex behavior, and it is the most valuable asset that is provided by a multiplicity of channels. The variety of situations calls for a variety of responses. For example, after a shock the "decision" for an octopus is not simply to "retreat," but how fast and how far to go, whether to emit ink, whether to show the dymanic pattern or whether to roll up into a ball with suckers outwards. The varying output from the matrices must provide for such decisions, but we have no idea how they are made.

The vertical lobe circuit and tactile memory

The interest of these systems of matrices is greatly increased by the fact that they occur also in the chemo-tactile memory system that is present in octopods (but not in decapods). This is served by four lobes precisely paralleling those of the visual sys-

tem (see Wells, 1978; Young, 1983). However, the two systems are not completely separate. It was soon found that removal of the vertical lobe impairs the efficiency of learned tactile discrimination (Wells & Wells, 1957). The tactile memory is thus served by passing signals through matrices in no less than eight lobes, which are discussed more fully elsewhere (Young, 1991). There is also a slight power of tactile learning in the suboesophageal lobes (Young, 1983). Cephalopods indeed provide us with excellent examples of distributed memory systems, involving multiple parallel channels. There is much more work to be done before we can properly understand how these matrices are used to produce such varied and successful behavior.

Conclusion

There is provision for the detection of light in all cephalopods, even those that live in the greatest depths. They vary greatly in the means for detecting it, and they make various uses of the information that results. By far the most subtle and varied are the responses of shallow water forms such as *Octopus*, *Loligo* and *Sepia* to the features of their complex surroundings. The mechanism of the retina and brain by which they do this, such as that of mammals, among the most intricate of all known physical systems. Nevertheless, we can begin to understand it, and this is thanks largely to the early work done by Brian Boycott.

Acknowledgment

I am very grateful for grants received from the University College, London, and also from the Wellcome Trust; to Professor L. Weiskrantz and the Department of Experimental Psychology in Oxford for accommodation; and to my wife Raye for secretarial help.

References

- ALDRED, R., NIXON, M. & YOUNG, J.Z. (1983). *Cirrothauma murrayi* Chun, a finned octopod. *Philosophical Transactions of the Royal Society B*, **301**, 1–54.
- BOYCOTT, B.B. (1961). The functional organization of the brain of the cuttlefish (*Sepia officinalis*). *Proceedings of the Royal Society B* **153**, 503–534.
- BOYCOTT, B.B. & YOUNG, J.Z. (1950). The comparative study of learning, *Symposium of the Society for Experimental Biology* **4**, 432–453.
- BOYCOTT, B.B. & YOUNG, J.Z. (1955). A memory system in *Octopus vulgaris* Lamark. *Proceedings of the Royal Society B* **143**, 449–480.
- CAJAL, S.R. (1917). Contribución al conocimiento de la retina y centros ópticos de los cefalópodos. *Trabajos del Laboratorio de Investigaciones Biológicas de la Universidad de Madrid* **15**, 1–82.
- GRAY, E.G. & YOUNG, J.Z. (1964). Electron microscopy of synaptic structure of *Octopus* brain. *Journal of Cell Biology* **21**, 87–103.
- HAEEFELFINGER, H. R. (1954). Inkretorische drüsenkomplexe im gehirn decapoder cephalopoden. *Revue Suisse de Zoologie* **61**, 151–162.
- HANLON, R.T. & MESSENGER, J.B. (1988). Adaptive coloration in young cuttlefish (*Sepia officinalis*): the morphology and development of body patterns and their relation to behavior. *Philosophical Transactions of the Royal Society B* **320**, 437–487.
- KOHONEN, T. (1988). *Self-Organization and Memory*. Springer-Verlag.
- MAURO, A. & BAUMANN, F. (1968). Electrophysiological evidence of photoreceptors in the epistellar body of *Eledone moschata*. *Nature* **220**, 342–343.
- MOODY, M.F. & PARRISS, J.R. (1961). The discrimination of polarized light by *Octopus*: a behavioral and morphological study. *Zeitschrift für vergleichende Physiologie* **44**, 268–291.
- NISHIOKA, R.S., HAGADORN, I.R. & BERN, H.A. (1962). Ultrastructure of the epistellar body of the octopus. *Zeitschrift für Zellforschung und mikroskopische Anatomie* **57**, 406–421.
- NISHIOKA, R.S., YASUMASU, I., PACKARD, A., BERN, H.A. & YOUNG, J.Z. (1966). Nature of vesicles associated with the nervous system of cephalopods. *Zeitschrift für Zellforschung* **75**, 301–316.
- ROLLS, E.T. (1990). Function of the primate hippocampus in spatial processing and memory. In *Neurobiology of Comparative Cognition*, ed. HOLTON, D.S. & KESNER, R.P., Hillsdale, New Jersey.
- SAIDEL, W.M. (1982). Connections of the *Octopus* optic lobe: an HRP study. *Journal of Comparative Neurology* **206**, 346–358.
- SAIDEL, W.M., LETTVIN, J.Y. & MACNICHOL, E.F. (1983). Processing of polarized light by squid photoreceptors. *Nature* **304**, 534–536.
- SEIDU, M. ET AL. (1990). On the three visual pigments in the retina of the firefly squid (*Watasenia scintillans*). *Journal of Comparative Physiology A* **166**(6), 769.
- SUTHERLAND, N.S. (1958). Visual discrimination of the orientation of rectangles by *Octopus vulgaris* Lamark. *Journal of Comparative Physiology and Psychology* **51**, 452–458.
- THORE, S. (1939). Beiträge zur Kenntnis der vergleichenden anatomie des zentralen nervensystems der dibranchiaten cephalopoden. *Pubblicazioni della Stazione Zoologica di Napoli* **17**, 313–506.
- WELLS, M.J. (1962). Early learning in *Sepia*. *Symposium of the Zoological Society* (London) **8**, 149–169.
- WELLS, M.J. (1978). *Octopus*. London; Chapman & Hall.
- WELLS, M.J. & WELLS, J. (1957). The effect of lesions to the vertical and optic lobes on tactile discrimination in *Octopus*. *Journal of Experimental Biology* **34**, 469–477.
- YOUNG, J.Z. (1929). Sopra un nuovo organo dei cefalopodi. *Bolletino della Società Italiana di Biologia Sperimentale* **4**, 1–3.
- YOUNG, J.Z. (1961). Learning and discrimination in the octopus. *Biological Review* **36**, 32–96.
- YOUNG, J.Z. (1964). *A Model of the Brain*. Oxford: Clarendon Press.
- YOUNG, J.Z. (1965). The organization of a memory system. The Croonian Lecture. *Proceedings of the Royal Society B* **163**, 285–320.
- YOUNG, J.Z. (1970). The stalked eyes of *Bathothena*. *Journal of Zoology* (London) **162**, 437–447.
- YOUNG, J.Z. (1971). *The Anatomy of the Nervous System of Octopus vulgaris*. Oxford: Clarendon Press.
- YOUNG, J.Z. (1983). The distributed tactile memory system of *Octopus*. *Proceedings of the Royal Society B* **218**, 135–176.
- YOUNG, J.Z. (1991). Computation in the learning systems of cephalopods. *Biological Bulletin* (in press).
- YOUNG, R.E. (1977). Ventral bioluminescent countershading in midwater cephalopods. *Symposium of the Zoological Society* (London) **38**, 161–190.
- YOUNG, R.E. (1978). Vertical distribution of photosensitive vesicles of pelagic cephalopods from Hawaiian waters. *Fisheries Bulletin* **76**, 583–613.
- YOUNG, R.E., ROPER, C.F.E. & WALTERS, J.F. (1979). Eyes and extraocular photoreceptors in midwater cephalopods and fishes. Their roles in detecting downwelling light for counterillumination. *Journal of Marine Biology* **51**, 371–380.