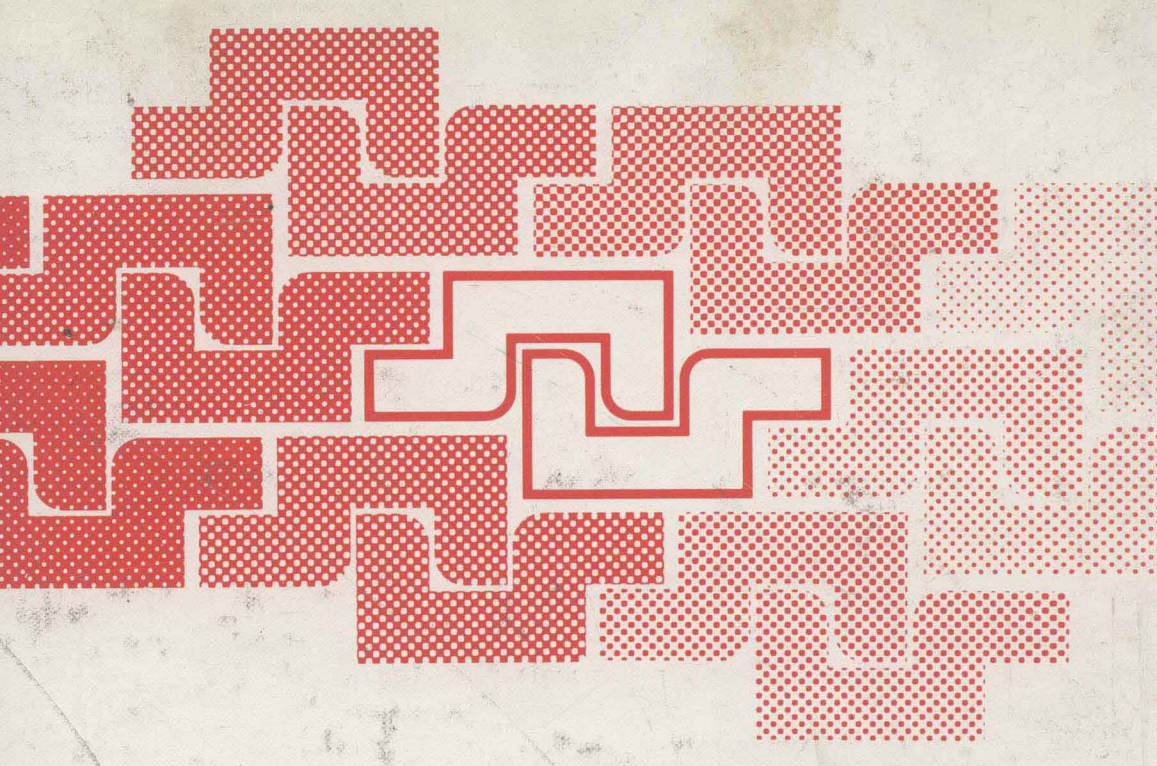

Nervous Systems in Invertebrates

Edited by

M. A. Ali

NATO ASI Series

Nervous Systems in Invertebrates

Edited by

M. A. Ali
University of Montreal
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PREFACE

The idea of holding an Advanced Study Institute (ASI) and getting a volume out, on the Nervous Systems in Invertebrates first cropped up in the summer of 1977 at the ASI on Sensory Ecology. I had prepared a review of the nervous systems in coelomates and noticed how much we depended on Bullock and Horridge's treatise on the one hand and how much new material and requirements has cropped up since 1965, when this classical work was published. Interest in the concerted study of pollution and environmental toxicology was growing in geometrical proportions and the use of invertebrates as indices was growing. As a teacher of a course on the biology of invertebrates since the beginning of my career I had also noticed how the interest of the students and the content of my course was shifting gradually and steadily from the traditional morphology-taxonomy type to the physiology-ecology-embryology orientation. Students were demanding to know the relevency of what they had to learn. Thus, after the ASI on Photoreception and Vision in Invertebrates held in 1982 the question of one on nervous systems was raised by a number of colleagues. It appeared then that the consensus was that the time was ripe to hold one and that it will be worthwhile. Therefore, as usual arrangements had to begin at least two years in advance. Most of the persons I contacted to lecture and write chapters on selected topics agreed enthusiastically. As is usual in the case of most ASIs, the programme had to be structured with the tutorial nature of the gathering and the ensuing volume in mind. This called for the selection of topics which were often imposed on the lecturers-authors. Also, as a NATO-ASI the choice of lecturers had to be made with as wide a national distribution as possible in mind. Of course, the reputation of the lecturer-author, his or her ability to present an interesting lecture and chapter and, his or her ability to get along with a heterogenous group over a two-week period had also to be taken into consideration. As the organiser, I was extremely lucky to gather a group of people who satisfied all these conditions as evidenced by the smooth way the ASI functioned. As I usually do, I asked the authors-lecturers to be as provocative and speculative as possible, especially in their oral presentations at the ASI. Most were so as evidenced by the lively discussions that ensued. At a meeting of the authors we ironed out the details and established general standards. Apart from the criticism the presentations received at the ASI, the finished products were also reviewed critically by the editor and at least one other competent person. As the organiser I attended every session and as editor read every chapter and learned a great deal about the matter and I hope that the users of this volume would find it of some use. The authors and I have tried to present the situation, as much as possible, as it reflects the actual state of affairs in this field. The concluding chapter, based on the rapporteur presentations and ensuing discussions which took place on the last day of the ASI tries to bring out as many perspectives as possible. We wanted to put in a glossary of terms but the constraints of time made this most impossible and I regret that it had to be so.

I am very grateful to my colleague Mary Ann Klyne for the help she

gave in the organisation of the meeting and the editing of the volume. I thank Catherine Joron of Jacmar Informatique Inc. for the preparation of the typescript. Françoise Simard and Miss Margaret Pertwee helped with the various aspects of the organisation. I am also very appreciative of the help that Nick Strausfeld and Michel Anctil gave in the choice of lecturers-authors. Michel Anctil also kindly helped with the preparation of the introductory chapter.

Financial assistance was provided to a large extent by the Scientific Affairs Division of NATO and I thank the director of the ASI programme, Craig Sinclair, for his encouragement throughout. Other financial help came from the Natural Sciences and Engineering Research Council of Canada, FCAR du Québec and the Université de Montréal. I thank Jean-Luc Grégoire, vice-principal and Marcia Boisvert, coordinator of events at Bishop's University for their help. The director of my department, Roch Carbonneau, extended the numerous facilities of the department to facilitate the organisation of the ASI. My editor at Plenum Press, Patricia Vann has been patient, understanding and helpful and I am thankful to her for that.

Montréal, May 1987 M.A. ALI

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INTRODUCTION

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The invertebrates represent such a large chunk of the animal kingdom that their nervous systems simply cannot be ignored, would it be just to understand fundamental mechanisms of neuronal activity. This was understood decades ago by Hodgkin and Huxley, and Bullock working on the squid giant axon and synapses, by Kandel and his colleagues on the cellular neurobiology of learning and memory in Aplysia, etc. These efforts pioneered the model-oriented approach to the study of the invertebrate nervous systems.

The early realisation of the expository power of invertebrate neurobiological preparations led to the emergence of Bullock and Horridge's now classic monograph on the nervous systems of invertebrates. One had to take stock of what one knew of these nervous systems, their organisation and the behaviours they elicited and sustained, with an eye on disentangling from this mass of information new models most appropriate to shed light on neurobiological questions popping out by observing vertebrate, especially mammalian brains.

Although a few invertebrate model systems are exemplified in some of the contributions of this book, the main thrust of the latter is more in the tradition of Bullock and Horridge's approach. Its intent is to provide, on a reduced and somewhat more modest scale, a survey of the kinds of nervous systems that the invertebrates use to relate to their worlds, in order to get a feeling for the levels of understanding we have reached, and to highlight the riddles and puzzles and roadblocks which still succeed in preventing us from gaining a holistic understanding of the subject.

The first four chapters, in the vein of the first section of Bullock and Horridge's reference work, attempt to formulate general organisational principles regarding synaptic morphology (Westfall), synaptogenesis in cell culture (Bacon), cellular homologies as probes of the genealogy of identified neurones (Croll) and contemporary views on the role of glial cells (Pentreath). These chapters include issues that were largely of current interest for Bullock and Horridge in 1965, and yet remain so today with the advantage of having gained a deeper understanding of these topics in the meantime.

Bullock and Horridge had largely and deliberately ignored chemical neurotransmission in their monograph. Understandably so for reasons of

space and because of the poor state of knowledge on the subject at the time. They had, however, included a substantial chapter on neurosecretion. The field has bounced back to haunt them in the 80s, especially due to the emergence of neuropeptides as major players of chemical communication within the nervous system of invertebrates. Several of the following chapters deal with neurotransmitters and neurotransmitter-specific pathways in invertebrate nervous systems. General aspects of the neurochemistry and distribution of invertebrate neuropeptides are introduced by Grimmelikhuijzen, Graff, Groeger and McFarlane. Insects provide good examples of neuropeptidergic systems and these are examined by Thorpe and Duve, and Nässel in two chapters on the neurochemistry and cellular localisation of neuropeptides in intensively investigated insect species. In addition, Nässel's chapter examines the distribution of classical neurotransmitters such as monoamines and amino acids in the insect CNS.

The next 10 chapters are loosely modelled after the systematic accounts of the invertebrate groups in Bullock and Horridge's monograph. However, space limitations and the extraordinary growth of knowledge of these nervous systems since 1965 have forced us to be very topical and very selective in the treatment of anatomical and physiological aspects of the nervous system of only the major invertebrate taxa. The taxa covered are the Porifera, Cnidaria and Platyhelminthes (Satterlie and Spencer), Annelida (Blackshaw), Chelicerata (Munoz-Cuevas and Coineau), Crustacea (Laverack), Insecta (Nässel, Robertson), Cephalopoda (Marthy), Chaetognatha (Goto and Yoshida), Echinodermata (Cobb) and Tunicata (Bone). Major themes raised by these authors are the evolutionary emergence of centralisation in the nervous system, the neurophysiological analysis of circuits and the control of behaviour, the cellular basis of integration and chemical transmission, and developmental issues as related to ecological-ethological problems.

The last 4 chapters cover miscellaneous topics relevant to specific, neurally controlled activities of some invertebrate taxa. Yoshida, Nogi and Tani examine how the gonads of sea urchins function as neurally controlled effector systems. The light-emitting effectors of various invertebrate groups are reviewed by Anctil from the point of view of their nervous control. An insect sensory function of great behavioural import, the acoustical communication system of crickets, is presented by Schildberger. The book concludes with the exposition of a model of neuronal integration in the insect nervous system by Altman and Kien.

ULTRASTRUCTURE OF INVERTEBRATE SYNAPSES

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ABSTRACT

Invertebrate chemical synapses are characterized by a diversity of presynaptic vesicles and membrane-associated structures. They have in common with classical chemical synapses of vertebrates a pair of parallel densified membranes with a uniformly wide intercellular cleft containing intracleft material, a presynaptic aggregation of clear or dense-cored vesicles, and usually one or more mitochondria with nearby microtubules in the synaptic terminal or axonal varicosity. At these conventional synaptic foci some vesicles have thin filamentous connections to the presynaptic membrane. Invertebrate neuromuscular junctions often appear morphologically similar to interneuronal synapses because they lack the postsynaptic infoldings of vertebrate muscles. Electrical synapses presumably appear in all metazoa as morphologically identifiable gap junctions in which there is cytoplasmic continuity between two cells separated by a 2-3-nm-wide intercellular gap. In addition to these conventional synapses there are dyads, spine synapses, neurosecretory-motor junctions, neuromuscular junctions with presynaptic dense bars, and gap junctions with vesicles in various invertebrate groups.

1. INTRODUCTION

Synapses are sites of rapid and precise information transfer between cells and are characterized ultrastructurally by parallel, close apposition of a pair of membranes. Chemical synapses presumably are present in all animal plyla with a nervous system and, in general, are characterized by vesicle-associated, paramembranous densities separated by a 15 to 30-nm-wide intercellular cleft. Information transfer occurs at these synapses as a result of release of a chemical by one neuron onto the surface of another neuron or effector cell.

The ultrastructure of invertebrate synapses is poorly understood compared to that of vertebrate synapses. Invertebrate synaptic foci or active zones often lack the striking presynaptic dense projections and

postsynaptic densities characteristic of typical central synapses in vertebrates. Moreover, there may be only a few large irregular vesicles, often with dense cores, at invertebrate synaptic foci instead of the large aggregations of small, clear vesicles that are clustered at active zones in the vertebrate brain. Also, in invertebrate nervous systems, neurosecretory neurons can form synaptic contacts on other neurons and effector cells in addition to synaptoid contacts on noncellular lamellae.

Electrical synapses presumably appear in all metozoa as morphologically identifiable gap junctions in which there is cytoplasmic continuity between two cells separated by a 2 to 3-nm-wide intercellular gap. Gap junctions typically lack synaptic vesicles, except at septal synapses between giant axons of earthworms and crayfish. Electrical information transfer occurs between cells at these morphologically specialized junctions.

In 1978, Cobb and Pentreath analyzed the comparative morphology of invertebrate and vertebrate synapses and concluded that specialized chemical synapses are the exception rather than the rule in invertebrates. The present phylogenetic survey of synaptic morphology in invertebrates suggests that specialized chemical synapses are the rule in invertebrates, but that we need more investigations at a detailed ultrastructural level. Improved techniques of fixation and higher magnifications of serial sections through active synaptic foci in a variety of neural regions, both central and peripheral, will add greatly to our current knowledge of invertebrate synaptic structure.

2. CHARACTERISTICS OF INVERTEBRATE SYNAPSES

Invertebrate chemical synapses are characterized by a diversity of presynaptic vesicles and membrane-associated structures. They have in common with classical chemical synapses of vertebrates a pair of parallel, densified membranes with a uniformly wide, intercellular cleft containing intracleft material, a presynaptic aggregation of clear or dense-cored vesicles, and usually one or more mitochondria with nearby microtubules in the synaptic terminal or axonal varicosity. The paired synaptic membranes and intervening cleft are recognized by some increase in electron density owing to associated fine filaments, which in the cleft often appear as periodic striations (Figs. 1-4). Such junctional densities, when associated with a linear or stacked array of vesicles, represent sites of active synaptic foci. The triadic densifications of pre- and postsynaptic membranes and intracleft material are equal in length and constitute the synaptic membrane complex. The symmetry or asymmetry of the paramembranous densities is not a feature that can be discussed in invertrebrate chemical synapses where our knowledge is limited and the synaptic foci vary greatly in their morphology. Some synaptic membrane complexes have thick paramembranous densities, whereas others have only a thin densification of the paired membranes (Figs. 1-2). Also, some synaptic membrane complexes are long and continuous, whereas others have one or more short interruptions along their length (Figs. 2-3). Many are very short and extremely difficult to locate at low mangifications with the electron microscope (Figs. 1, 4). In some animals, such as jellyfish, two-way or symmetrical synapses are common (Fig. 5). Several groups of animals have dyadic type synapses with elaborate presynaptic bodies in association with two postsynaptic cells (Figs. 6-7). Other variations include a slightly widened cleft with an intermediate periodic line and mixed clear and dense-cored vesicles. In the polychaete annelid, there is a presynaptic dense body ringed with clear vesicles (Fig. 8). In cephalopods spine synapses are present in which a halo of clear vesicles surrounds a postsynaptic invagination (Fig. 9). Sometimes, dense-cored

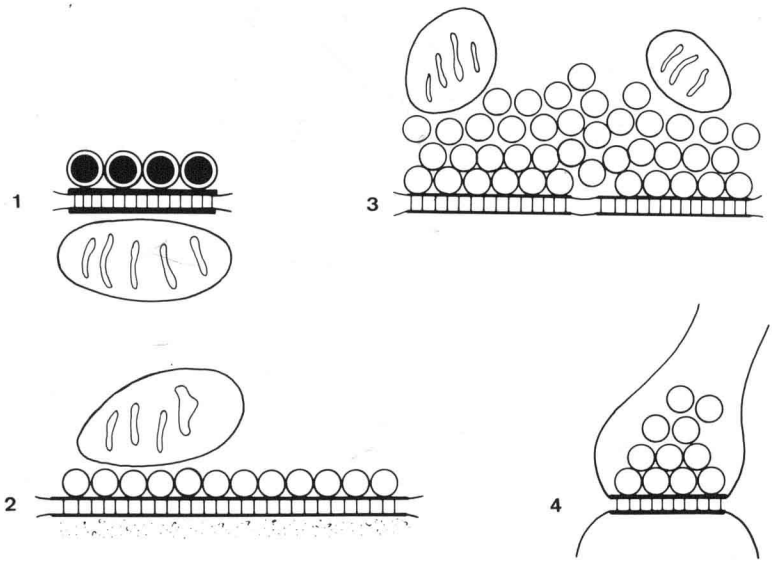


FIG. 1: Polarized, interneuronal synapse of Hydra (Hydrozoa, Cnidaria). A short, single row of dense-cored vesicles lies in contact with a presynaptic membrane density, which parallels the postsynaptic density and region of intracleft filaments. Such synapses occur en passant between axons and usually have a mitochondrion nearby (Westfall, original).

FIG. 2: Polarized, interneuronal synapses with mitochondria adjacent to a long, single row of clear vesicles paralleling a pair of thin, paramembranous densities with intracleft transverse filaments as observed in hydromedusae and jellyfish (Westfall, original).

FIG. 3: Polarized, interneuronal synapse with mitochondria adjacent to tiers of synaptic vesicles at a long, bipartite, synaptic membrane complex as seen in a larval mussel (Bivalvia, Mollusa). Note regular arrangement of initial row of vesicles at paired, synaptic membranes except for loss of continuity at interruption. After Zs-Nagy and Lábos (1969).

FIG. 4: Nerve terminal with tiered clear vesicles at a short, synaptic membrane complex in a sea urchin (Echinoidea, Echinodermata). After Cobb and Laverack (1966a).

vesicles are present in a synapse with predominently clear vesicles (Fig. 10). In other cases, neurosecretory-type granules predominate (Fig. 11). Occasionally, dense-cored vesicles are present at the presynaptic contact of a neurosecretory ending (Fig. 12). Neurosecretory endings may form true synaptic contacts or end in synaptoid contacts with small clear vesicles at an extracellular lamina (Fig. 13).

Invertebrate neuromuscular junctions often appear morphologically similar to interneuronal synapses because they lack the postsynaptic infoldings of vertebrate striated muscles and have a tendency to contact the granular cytoplasm of the underlying muscle cell. In some cnidarians, dense-cored vesicles may be present at the neuromuscular synapse.

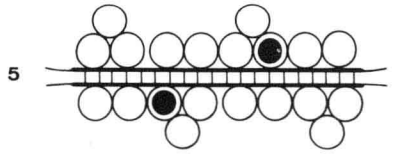


FIG. 5: Symmetrical or two-way interneuronal chemical synapse of the jellyfish Cyanea (Scyphozoa, Cnidaria). Note mixed clear and dense-cored vesicles on both sides of the synaptic membrane complex. After Horridge and Mackay (1962).

Usually the synaptic vesicles are clear and lie either in a single row closely apposed to the presynaptic membrane density or as tiers of vesicles (Figs. 14-15). In jellyfish, there is often a subsynaptic cisterna present at neuromuscular synapses (Fig. 16). Ctenophores have a unique, presynaptic triad of a row of vesicles, a flattened cisterna of endoplasmic reticulum, and a large mitochondrion at the neuromuscular synapses (Fig. 17). At some mollusc neuromuscular synapses, there are large aggregations of clear vesicles (Fig. 18). Synaptic vesicles generally are few in number at echinoderm neuromuscular junctions, where clear vesicles predominate at the presynaptic membrane (Fig. 19). In arthropods, the synaptic vesicles congregate at one or more hour glass-shaped, presynaptic dense bodies (Figs. 20-21). The neuromuscular cleft, usually of similar width to the interneuronal cleft, may be bisected by an intermediate periodic line (Figs. 18, 20-22) and/or contain faint cross filaments (Figs. 14-19). In ctenophore, earthworm, moth, lobster and crayfish neuromuscular synapses, a row of periodic filaments has been observed on the extracellular surface of the postsynaptic membrane (Figs. 17, 20, 23). In both crayfish and lobster, excitatory neuromuscular junctions can be distinguished from inhibitory neuromuscular junctions on the basis of their ultrastructure. Excitatory junctions have an abundance of clear, round vesicles, whereas inhibitory junctions contain fewer and less regular vesicles (Figs. 23-23).

Electrical synapses vary from typical gap junctions with a 2-3-nm-wide gap between a pair of parallel, closely apposed membranes in coelenterates (Fig. 24) to a somewhat wider gap with ribbed membranes and associated vesicles between giant axons of crayfish (Fig. 25). Although the junctions between giant axons sometimes appear to have the morphology of chemical synapses, there is electrophysiological evidence that they are low resistance junctions.

This brief ultrastructural survey of invertebrate synapses indicates that they have in common a uniformly constant apposition of paired membranes for each specialized synaptic contact but that there is great morphological diversity among synaptic components. Conventional synapses with paired densified membranes and associated vesicles constitute the majority of synapses found in all animal phyla with a nervous system, whereas unusual configurations such as dyads and synaptic spines are usually associated with sensory receptor cells. Large aggregations of neurosecretory granules and dense-cored vesicles generally occur in neuroendocrine organs.

The morphology and occurrence of different types of synapses in the primitive nerve net of cnidarians will be discussed next, followed by a selected review of synaptic variations described in several higher invertebrate groups.

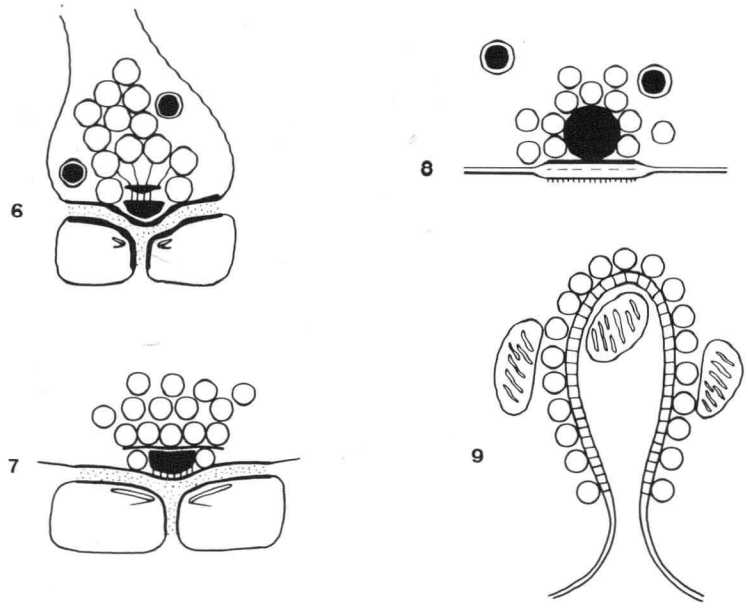


FIG. 6: Dyad with presynaptic clear and dense-core vesicles and pair of postsynaptic neurites with small cisternae of endoplasmic reticulum in the flatworm Gastrocotyle (Monogenea, Platyhelminthes). Note halo of clear synaptic vesicles with filamentous connections to a bipartite, presynaptic dense bar, intracleft density, and paired membrane thickenings. After Shaw (1981).

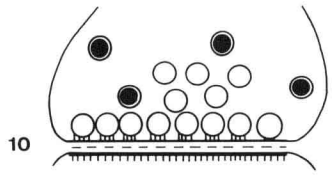
FIG. 7: Dyad with presynaptic clear vesicles and pair of postsynaptic elongate cisternae with medial whiskers in the fly eye (Insecta, Arthropoda). Note row of vesicles along top plate of synaptic bar. After Burkhardt and Braitenberg (1976).

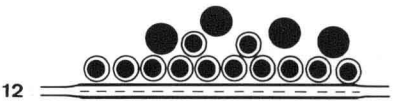
FIG. 8: Presynaptic dense body surrounded by clear vesicles with slightly larger, dense-cored vesicles nearby in Nereis (Polychaeta, Annelida). Note intermediate, periodic line in widened cleft and postsynaptic specialization. After Dhainaut-Courtois and Warembourg (1969); Fisher and Tabor (1977).

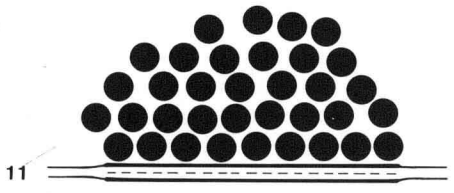
FIG. 9: Postsynaptic spine with associated mitochondria in the octopus statocyst (Cephalopoda, Mollusca). Note arrangement of presynaptic clear vesicles along invaginated, synaptic cleft with transverse filaments. After Budelmann and Thies (1977).

3. CNIDARIA

Synapses in the cnidarians, the most primitive group of animals with a recognizable nervous system, range from short foci of parallel electron dense membranes with one to three or four dense-cored or clear vesicles in Hydra (Fig. 1) to long foci of many vesicles in various jellyfish (Fig. 2). Symmetrical synapses were reported first in the marginal ganglia of the jellyfish Cyanea (Horridge et al. 1962; Horridge and Mackay 1962) and were thought to transmit bidirectionally, similar to electrical synapses between giant fibers in earthworms and crayfish. This was the first







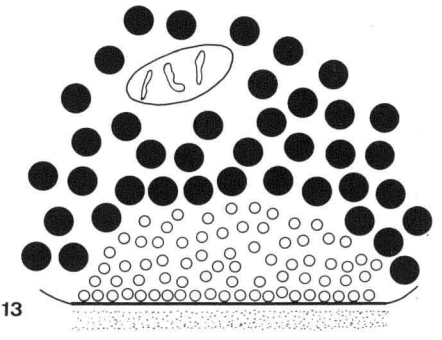


FIG. 10: Conventional interneuronal synapse with mixed clear and dense-cored vesicles in a gastropod mollusc. Note filamentous connections between initial row of clear vesicles and presynaptic membrane, an intracleft intermediate periodic line, and cytoplasmic densities on the postsynaptic membrane. After Coggeshall (1967).

FIG. 11: Interneuronal synapse with neurosecretory granules in Aplysia (Gastropoda, Mollusca). Note association of initial row of granules with synaptic membrane complex and intermediate, periodic line in slightly widened cleft. After Tremblay et al. (1979).

FIG. 12: Interneuronal synapse with dense-cored vesicles at the presynaptic membrane of a neurosecretory neuron in Aplysia. After Tremblay et al. (1979).

FIG. 13: Diagrammatic representation of a neurosecretory cell synaptoid contact on a noncellular lamella in crayfish (Crustacea, Arthropoda). Note mitochondrion among neurosecretory granules and small clear vesicles indicative of site of neuroendocrine release and vesicle recycling. After Bunt (1969).

report of vesicles on both sides of a 20-nm-wide synaptic cleft with parallel electron-dense membranes resembling vertebrate chemical synapses. The vesicles, 50-100 nm in diameter with an occasional electron-dense core, were closely apposed to the electron-dense membranes (Fig. 5). Recently, Anderson (1985) demonstrated physiologically that such synapses in the motor nerve net of Cyanea are bidirectional chemical synapses.

Polarized or unidirectional synapses in cnidarians were demonstrated ultrastructurally by Jha and Mackie (1967) in the marginal nerve ring of the hydromedusan Sarsia. Small tiers of clear and dense-cored vesicles (100-150 nm in diameter) were aggregated at membrane densities with a

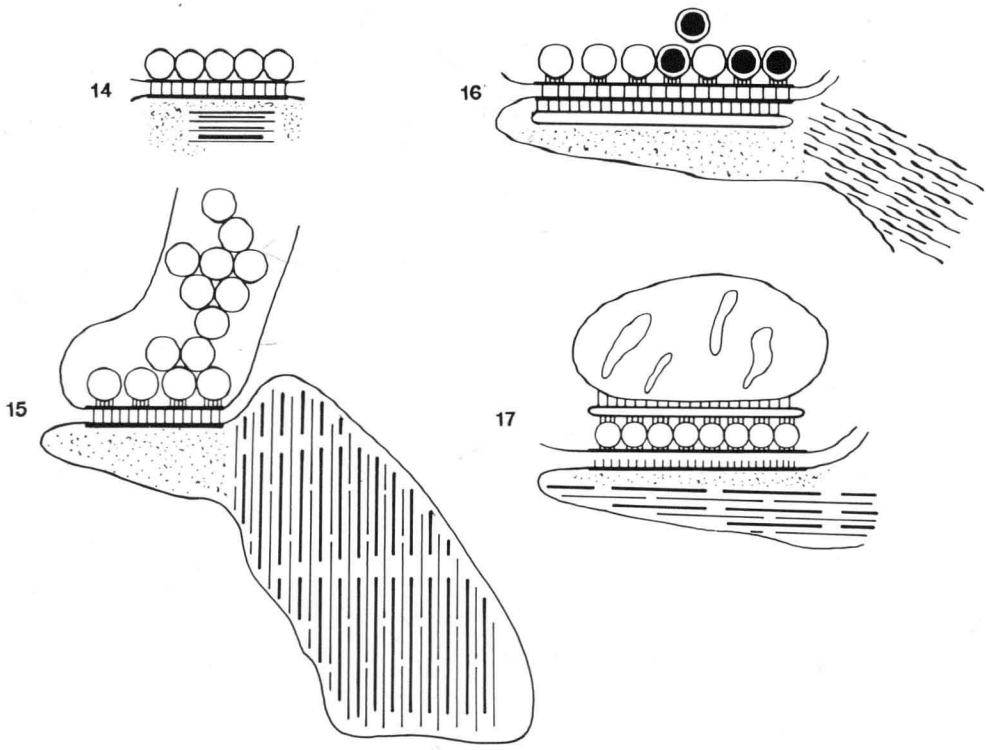


FIG. 14: En passant neuromuscular synapse with myonemes near a straight, postsynaptic membrane in the hydromedusan Aglantha (Hydrozoa, Cnidaria). Note short, single row of presynaptic clear vesicles paralleling paramembranous densities and intracleft filaments. After Singla (1978a).

FIG. 15: Nerve terminal synapse on a muscle cell process in the sea anemone Metridium (Anthozoa, Cnidaria). Note tiered arrangement of presynaptic clear vesicles and postsynaptic granular cytoplasm at contact site with longitudinal muscle. After Westfall (1970b).

FIG. 16: Neuromuscular synapse with mixed vesicles and a subsynaptic cisterna of endoplasmic reticulum observed in the jellyfishes Aurelia, Chrysaora, and Haliclystus (Scyphozoa, Cnidaria). Westfall, original.

FIG. 17: Ctenophore neuromuscular synapse with a presynaptic triad of mitochondrion, flattened cisterna of endoplasmic reticulum, and single row of clear vesicles at the presynaptic membrane. Note filamentous connections between presynaptic elements; postsynaptic membrane densification is periodic within the cleft. After Hernández-Nicaise (1968; 1973a).

20-nm-wide cleft between neurites. Buisson and Franc (1969) observed a single row of 100 to 150-nm-diameter vesicles at en passant synapses between neurites in the anthozoan Veretillum. Although Hydra was said to be the exception to the rule that cnidarians have synapses (Bullock and Horridge 1965), Westfall et al. (1970a, 1971) found ultrastructural evidence of synaptic foci with vesicles on one or both sides of paired,

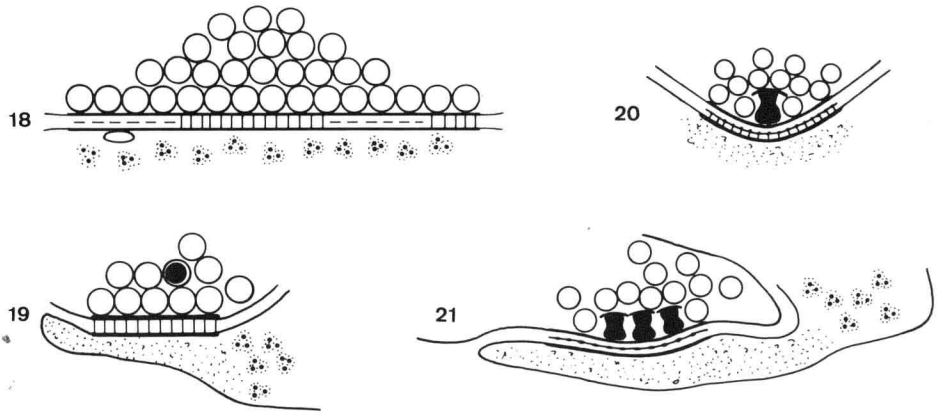


FIG. 18: Large neuromuscular synapse with tiered mass of presynaptic clear vesicles in the fresh water mussel, Anodonta (Bivalvia, Mollusca). Note long synaptic membrane complex with variable, intermediate line or cross filaments in cleft. After Zs-Nagy and Lábos (1969).

FIG. 19: Neuromuscular synapse on a winglike extension of muscle cell in a sea urchin (Echinoidea, Echinodermata). Note initial row of clear vesicles and single, dense-cored vesicle in second row of short tier of presynaptic vesicles. After Cobb and Laverack (1967).

FIG. 20: Presynaptic dense bar observed at annelid, moth, and lobster neuromuscular synapses. Note clear vesicles surrounding hour-glass-shaped presynaptic density, intermediate line in cleft, and periodic filaments on extracellular surface of postsynaptic membrane. After Rosenbluth (1972); Rheuben and Reese (1978); Govind and DeRosa (1983).

FIG. 21: Neuromuscular synapse on granular, cytoplasmic extension of muscle cell in a lobster (Crustacea, Arthropoda). Note clear vesicles associated with row of presynaptic, hour-glass-shaped densities paralleling intracleft intermediate line and postsynaptic density. After Govind and Pearce (1982).

parallel, electron-dense membranes between both neuronal soma and axons in this simple hydrozoan polyp. Thus, all cnidarians presumably have chemical synapses, but not all types of synapses have been well studied to date. Two difficulties are apparent in surveying the ultrastructural literature on cnidarian synapses. First, many investigators do not publish high magnification micrographs of their synapses, so morphological criteria cannot be well defined. Secondly, preservation of cnidarian tissues for electron microscopy is difficult, so that measurements of synaptic vesicles often are variable owing to vesicular swelling or other shape changes. In spite of these difficulties, I believe there is good ultrastructural evidence for interneuronal, neuromuscular, and neuronematocyte synapses in addition to neurosecretory endings and gap junctions in the cnidarian nervous system.