# SYNAPSES IN THE CENTRAL NERVOUS SYSTEM*

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PLATES 64 TO 66

The cytological problems presented by the synapse were carefully considered by Bodian (6) in his review of 1942. He indicated that it is desirable to know more about "the ultrastructure of the membranes concerned, the quantitative relations existing between surfaces of axon terminals and the surfaces of cells of termination, the intimate relationships of myelin and of glia to synaptic surfaces, the types, approximate numbers, and specific sites of origin of endings on cells of each type, the electrical properties of cellular elements and intracellular materials, and the localized concentrations and site of action of both drugs and physiological substances which may produce or modify neuronal excitation, under varying conditions." Thanks to recent advances in neurophysiology (11), neuropharmacology (12, 22), and neuroanatomy, it is now possible to give answers to some of these problems, although the answers are by no means complete. The following paper reports an electron microscopic study of synaptic terminals in the medulla oblongata, cerebellar cortex, and cerebral cortex of the rat. The information presented is not sufficient for generalization to all types of synapses, but a remarkable uniformity in architecture and internal structure has been found among the morphological types of junctions studied. It remains to be seen whether this uniformity can be extended to synapses in all parts of the nervous system and to synapses with different pharmacological and physiological properties.

In addition to the preliminary report on similar synapses in abstract form (20), a number of electron microscopic studies of other synapses has appeared in the past few years. Robertson has studied axo-axonic synapses in the stellate ganglion of squid and in the abdominal ganglia of crayfish (27) as well as neuromuscular junctions in the chameleon (28). Sjöstrand (31) has examined the complex junctions between the rod cells and bipolar cells in the retina of

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the guinea pig. De Robertis and Bennett (9, 10) have described axo-somatic synapses in the sympathetic ganglia of the frog and axo-somatic and axo-dendritic synapses in the neuropil of the nerve cord of the earthworm. All of these reports have agreed on the essential character of these junctions: that there is a discontinuity between the cytoplasms of the pre- and postsynaptic elements, each of which is surrounded by its own cell membrane. An additional characteristic element that has been noted by several investigators (9, 13, 20) is a collection of fine vesicles in the presynaptic cytoplasm.

## *Materials and Methods*

The nervous tissue was fixed *in situ* in the living, anesthetized (sodium pentobarbital), adult rats by an injection of 2 or 3 per cent, chilled osmium tetroxide (buffered to pH 7.4–7.5 with acetate-veronal buffer (17)) into the fourth ventricle. Darkened fragments of medulla, cerebellum, and cerebrum were excised and cut into small fragments which were transferred to chilled osmium tetroxide and kept at 4°C. for 2 hours. The fragments were dehydrated by passage through increasing concentrations of methanol and embedded in *n*-butyl methacrylate catalyzed by the addition of 2 gm. luperco CDB per 100 ml. of monomer. Polymerization took place over a 12 hour period at 47°C. Thin sections cut by means of glass knives on a Servall microtome (24) were floated upon 20 per cent acetone and picked up on formvar-coated 150 mesh copper grids. An RCA EMU-2E electron microscope fitted with a 25 to 30 $\mu$ objective aperture was used. Micrographs made at an initial magnification of 4,000 to 12,000 were photographically enlarged approximately 5 times for study.

## OBSERVATIONS

The recognition of terminal junctions between neurons in electron micrographs presents a problem because it is usually not possible to trace within a given section or even a series of sections an entire nerve fiber from its origin to its end. It is well to recall in this connection that the concept of the synapse is partly a morphological and partly a physiological concept. The synapse signifies a special type of polarized apposition or junction of two nerve cells which has the particular property of transmitting nervous impulses from one cell to the other. Therefore, it is reasonable to seek in the electron micrographs for structures along the surfaces of perikarya and dendrites which have a peculiar, characteristic, polarized, internal organization. An invaluable clue provided by light microscopy is that the synaptic terminals of axons contain a remarkable concentration of mitochondria. This characteristic was noted in the earliest descriptions of end-feet or boutons terminaux (1, 14, 15) and has been confirmed for several types of synapses (2, 4, 5, 6). As these end-feet are examples of the simplest type of synaptic terminal, the one most readily recognized, they serve as a good starting point in a morphological analysis of the synapse in the central nervous system.

Fig. 1 is an electron micrograph of a section through a dendrite and its environs from the neuropil of the abducens nucleus in the rat. The surface of the dendrite appears as two, roughly parallel, undulating lines, 1.9 to 2.6 $\mu$ apart,

which at intervals turn outward at the roots of dendritic branches. Within the dendrite are numerous, long, tubular elements of the endoplasmic reticulum, about 180 A wide and remarkably straight. At irregular intervals they are dilated into chains of vesicles of various diameters. Occasional clusters of small, dense granules, 50 to 60 A in diameter, lie among these canaliculi, especially at the bases of branches. These granules represent small clusters of basophil material corresponding to the small clumps of Nissl substance seen particularly at sites of dendritic branching in stained sections examined with the light microscope (19, 21). The profiles of mitochondria are distributed in the peripheral cytoplasm of the dendrite, arranged with their long axes parallel to the length of the dendrite. These profiles show the usual internal configuration of mitochondria (18, 32), except that their cristae are arranged longitudinally rather than transversely.

Against both margins of the dendrite lie several small ovoid profiles that can be recognized as sections through end-feet or terminals by means of the concentration of mitochondria within them. In favorably oriented sections the telodendron can be found approaching the dendrite and broadening into a rounded ending ($T_4$). The larger ending ($T_1$) below the dendrite in Fig. 1 contains nine mitochondrial profiles, and the smaller endings above the dendrite ($T_2$, $T_3$) each contain three or four mitochondrial profiles. Comparable areas in the dendrite contain no more than two mitochondrial profiles. The mitochondria of the terminals have the usual smooth outer and folded inner membranes, but, as appears commonly in the nervous system (21), their inner folds or cristae are oriented longitudinally instead of transversely.

In addition to the aggregation of mitochondria, the internal structure of the end-feet presents another distinguishing feature. This is the collection of minute circular profiles, each about 200 to 650 A in diameter. Each profile is formed by a dark circular line, 50 to 70 A thick, which delimits a space containing homogeneous material slightly denser and occasionally much denser than the surrounding cytoplasmic matrix. The circular profiles are scattered throughout the ending either singly or in clusters, and in some instances they occupy the entire area of the ending that is not taken by mitochondria. Although such circular profiles occur occasionally and singly in axons and dendrites, they appear in large numbers and in great concentration only in the axonal terminals. Examination of numerous single sections and a few serial sections of endings indicates that the profiles of these structures are nearly always circular no matter how the plane of section is oriented with respect to the long axis of the terminal. Therefore, the profiles probably represent, in three dimensions, membranous spheres or vesicles containing an internal substance that is less dense than the membranes. These synaptic vesicles were described almost simultaneously by Palade and Palay (20) and by DeRobertis and Bennett (9, 10) in synaptic junctions from widely different sources. They

have also been noted in the neuropil of the thalamus by Fernández-Morán (13). Because of their universal presence in all presynaptic terminals that have been studied, there is some justification for thinking that these vesicles represent an essential and characteristic feature of the synapse.

A third component within the axonal terminal consists of occasional strands of regular, elongated profiles, sometimes appearing singly and sometimes in small sheaves ($T_1$ and $T_2$ in Fig. 1 and Fig. 2). These structures appear to be the ends of long, tubular or canalicular, membranous elements of the endoplasmic reticulum, which occur not only in the dendrite where they are profuse, but also in the axon where they are relatively sparse. Axon filaments and fine dense granules such as appear in other parts of the neuronal cytoplasm are absent from the axonal terminal.

The surface membrane of the presynaptic terminal is a continuation of the surface of the axon and its telodendron. In the micrographs it appears as a single continuous smooth line. As we would expect from light microscopy (6), there is no hint of a myelin sheath around the ending. In synapses studied by light microscopy the terminal enlargement appears to be separated from the postsynaptic cell or dendrite by a deeply stained membrane known as the "synaptolemma." It has been assumed that this synaptolemma is really an intimately apposed pair of membranes one of which belongs to the presynaptic element and the other to the postsynaptic cell. The electron micrographs (Figs. 1 and 2) show that this assumption is indeed the case. The base of each ending is closely apposed to the surface of the dendrite, following faithfully for a short distance the small indentations and undulations of its surface, but clearly separated from the dendrite by a space approximately 200 A wide. At no point do the limiting membranes of the ending and dendrite fuse. This intrasynaptic space is, furthermore, continuous with the interstitial space between neighboring cellular processes. Sometimes vague and irregular densities can be seen within the intrasynaptic space; sometimes threadlike material extends across the space, but usually it is devoid of discernible structure. When the contact of the terminal and dendrite or neuron extends over a considerable distance as, for example, in the junctions of large boutons terminaux or climbing fibers, the apposition of the two limiting membranes may be interrupted at one or more points by the interposition of glial processes or possibly portions of another ending. In Fig. 2, a long zone of contact between an expanded end-foot and the dendrite is interrupted at $x$ by the withdrawal of the basal limiting membrane of the ending from the surface of the dendrite in order to form a tunnel-like passage through which two glial fibers pass. A similar appearance is provided in Fig. 1 along the synaptic interface of terminal $T_3$.

At irregular intervals, the two apposed limiting membranes display roughened thickenings and increased densities which probably represent specialized patches in their structure. These dense patches resemble the altered surfaces of

epithelial cells at junctional sites with their neighbors, such as the terminal bars of intestinal epithelia, the desmosomes of stratified squamous epithelia (23), and the intercalated discs of cardiac muscle (33). However, the filamentous tufts seen in the epithelial junctions are not ordinarily present at the neural synapse. Instead, the small vesicles frequently cluster against the presynaptic membrane at these sites, and in favorably oriented sections they occasionally can be seen to open onto the intrasynaptic space.

End-feet terminating upon the surface of a perikaryon display all the features of those associated with dendrites (Fig. 3). The presynaptic mitochondria and vesicles differ in no way from those in terminals at other sites. The spacing of terminals upon the surface of neurons is of considerable interest but has not been studied carefully in the electron microscope. On the surfaces of some neurons the terminals are closely packed, one next the other, with only the usual narrow space between neighboring elements (as between terminals $T_2$ and $T_3$ in Fig. 1). Upon the surfaces of other neurons the terminals are more widely spaced. In fact, on the surface of the perikaryon pictured in Fig. 3 only one end-foot may be seen over its entire extent within the thickness of the section examined. In Fig. 3 a number of mitochondria lie beneath the synaptolemma. Although no special structures are evident under the postsynaptic membrane, the tendency of mitochondria in dendrites and perikarya to lie close to the surface may represent an orientation with reference to the synaptic sites, such as has been noted on the sarcoplasmic side of the neuromuscular junction (8, 20, 28).

One of the more complex axo-dendritic synapses is illustrated in Fig. 4. This micrograph represents a section through a glomerulus in the neuropil of the dorsal cochlear nucleus. Glomeruli in the granular layer of the cerebellar cortex possess the same structure. Most of this figure is occupied by a large, expanded, and branching axon terminal, which apparently enters the field through a narrow process from the right. Profiles of mitochondria crowd the center of this terminal and also appear in the branches shown at the upper margin of the picture. The rest of the axoplasm is strewn with small vesicles of assorted sizes (240 to 520 A, but most of them 300 A in diameter). Surrounding the central mass of the terminal and among its branches are several small dendritic tips, each containing one or more mitochondria, but devoid of small vesicles. The two component members of this synapse are separated from each other by a space about 200 A wide, and at irregularly placed sites, the apposing limiting membranes appear slightly thickened and denser than elsewhere. Thus this complex synapse, which has been so difficult to analyze in sections impregnated with silver and examined in the light microscope (6), proves to have essentially the same structure and—what is particularly evident—the same internal organization as have the simpler and more readily analyzed boutons terminaux.

In other synaptic fields, such as the molecular layer of the cerebellar cortex and in the cerebral cortex, formations with this essential structure also appear. In these regions, the axon terminals are small and contain only a few mitochondria and a cluster of vesicles located near a thickened limiting membrane in apposition to a typical dendritic process. The neuropil about nuclei in the medulla oblongata consists of a jumble of axons and dendrites among which appear pairs of axonal terminals and dendrites having the same structural features that have been described above. Similar formations have been noted by Fernández-Morán (13) in the neuropil of the thalamus.

## DISCUSSION

The synaptic junctions described in this paper belong to the two categories listed by Ramón y Cajal (25), axo-somatic and axo-dendritic junctions. Both of these types of synaptic apparatus have the same fundamental architectural plan. A third category, the axo-axonic synapse, has not yet been studied electron microscopically in the mammalian central nervous system, but in those situations where the presynaptic terminal resembles the end-foot or end-bulb of Held, it is reasonable to expect that the internal organization would also be the same. It would be interesting to know whether the presynaptic spiral fibers about the axons of sympathetic ganglion cells have a similar fine structure.

Three essential structural features characterize the synapses studied in this paper: (*a*) the closely apposed limiting membranes of the presynaptic ending and the postsynaptic cell or dendrite; (*b*) the cluster of mitochondria; and (*c*) the collections of fine vesicles filling the presynaptic terminal. The absence of protoplasmic continuity across the contact surface between the two members of the synaptic apparatus is impressive confirmation of the neuron doctrine enunciated and defended by Ramón y Cajal during the early part of this century (26). The separation between the two limiting membranes is only about 200 A, and, although the membranes occasionally are more widely separated to permit passage of glial processes or the telodendra of other nerve fibers, no glial or other protoplasmic material appears between them in regions of closest contact. The nature of the material filling this intrasynaptic cleft is unknown. The irregular or filamentous densities occasionally appearing within the space may represent precipitated interstitial ground substance or cement, or they may represent some specific substance released from the apposed surfaces. Experimental stimulation of the afferent nerve fibers may be expected to elucidate the nature of this material. The thickened dense patches in the two apposed membranes may be interpreted in two ways. (*a*) They may be points of adhesion between the two surfaces, analogous to similar differentiations of the surface membranes at the terminal bars and desmosomes of epithelial cells. Nerve endings are well known to be sticky (7) and to resist retraction from the cell of termination by shrinkage in fixed preparations. (*b*) The dense patches

may also be considered as the ultimate points for transmission of the nervous impulse. Suggestive support for this interpretation derives from the tendency for the minute vesicles within the bouton terminal to cluster at the presynaptic surface of the dense patches. Of course, it is conceivable that both interpretations may be equally pertinent. Only studies of experimentally produced changes can substantiate these suggestions or indicate others more valid.

The synapse as described in this paper is clearly polarized in its fine structure, as its definition leads us to expect. On the presynaptic side of the synaptolemma a collection of mitochondria and small vesicles occurs, whereas on the postsynaptic side no characteristic orientation or aggregation of cytoplasmic elements appears. The significance of this presynaptic constellation can only be surmised at present. As far as the mitochondria are concerned, their importance in the respiratory activity of the cell is too well known to require comment here (30). The correlation between the concentration of mitochondria in synaptic areas (1, 2, 4, 5, 6, 14, 15, 29) and the activity of enzymes involved in oxidative phosphorylation (16) in such regions is rather clear. On the basis of the implication of mitochondria in ion transport (3, 34), one may presume that their presence at the synapse has something to do with the electrical phenomena occurring here.

The clusters of small vesicles may have an even more direct role in the transmission of nervous impulses across the synapse. If an analogy may be drawn between these synaptic terminals and the myoneural junction which has essentially the same structure (20, 28), the small vesicles may be considered as containing small units of a chemical transmitter, like acetylcholine, or precursor of this transmitter, which are discharged into the intrasynaptic space. The physiological evidence for a particulate apparatus for discharge of acetylcholine at the myoneural junction is summarized by Fatt in a recent review (11) from which the following passage is quoted.

"In considering (the mechanism of release of a transmitter substance at junctions) it should first be noticed that in probably all preparations the release of transmitter would occur as the result of activity in a large number of discrete subcellular units in the terminals of the prejunctional fiber. The presence of such units is indicated in experiments on the vertebrate neuromuscular junction. When electric potentials are recorded at the individual junctional regions of muscle fibers, there is usually found a continuous display of randomly recurring pulses, each exhibiting all the characteristics of junctional activity. These pulses, obtained in the absence of any propagated impulse in the nerve, arise from the intermittent release of small quantities of acetylcholine from nerve terminals. The receptive region of the muscle fiber from which the potentials are recorded serves merely as a sensitive detector of this substance. The amplitudes of the spontaneous pulses are only about one-hundredth of the amplitude of the junctional response to a nerve impulse, and are scattered about their mean with a coefficient of variation of about 30 per cent. Hence it may be concluded that the apparatus for the release of acetylcholine at a junction is subdivided into a large number of units (at least 100), each of which is able to operate independently of the rest. As judged by the relatively small variations in the amplitude of spontaneous responses, the effectiveness of

different units at a particular junction is fairly uniform—at least within a factor of two. As yet no structure has been recognized, in the careful morphological studies that have been made of the neuromuscular junction, which might be identified with the prejunctional unit."

The heretofore unrecognized structure demanded by these physiological data may be the small vesicles which crowd the axon terminals, cluster at the junctional surface, and open onto the intrasynaptic space. A somewhat similar suggestion has been put forth by De Robertis and Bennett (10). As noted before, experimental evidence is needed to substantiate this suggestion.

## SUMMARY

A number of different synapses have been described in the medulla, cerebellar cortex, and cerebral cortex of the rat. All of these possess the same fundamental fine structure as follows:

1. Close apposition of the limiting membranes of presynaptic and postsynaptic cells without any protoplasmic continuity across the synapse. The two apposed membranes are separated by a cleft about 200 A wide, and display localized regions of thickening and increased density.

2. The presynaptic expansion of the axon, the end-foot or bouton terminal, contains a collection of mitochondria and clusters of small vesicles about 200 to 650 A in diameter.

Although the significance of these structures in the physiology of the synapse is still unknown, two suggestions are made: that the mitochondria, by means of the relation between their enzymatic activity and ion transport, participate in the electrical phenomena about the synapse; and that the small synaptic vesicles provide the morphological representation of the prejunctional, subcellular units of neurohumoral discharge at the synapse demanded by physiological evidence.

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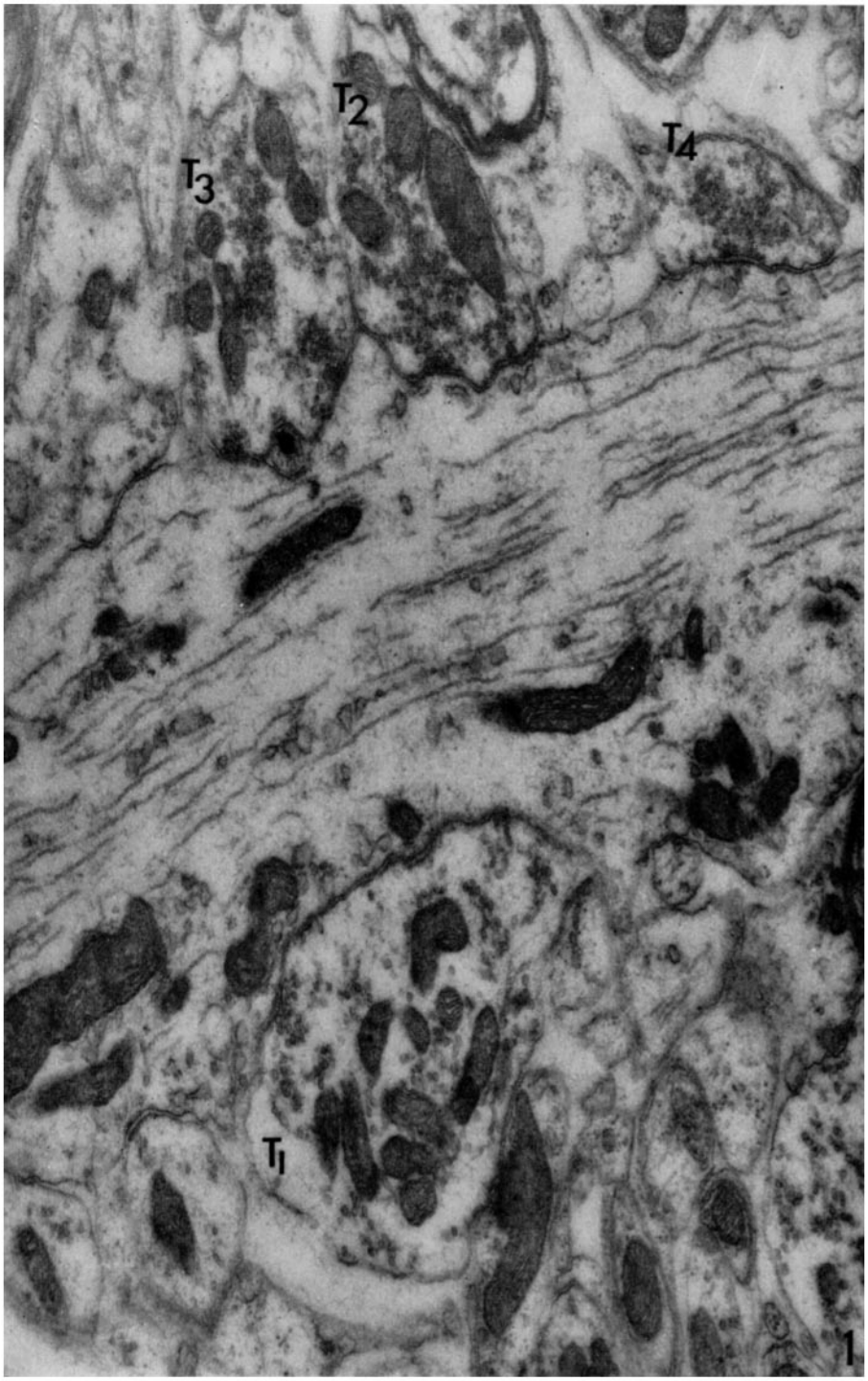
## EXPLANATION OF PLATES

### PLATE 64

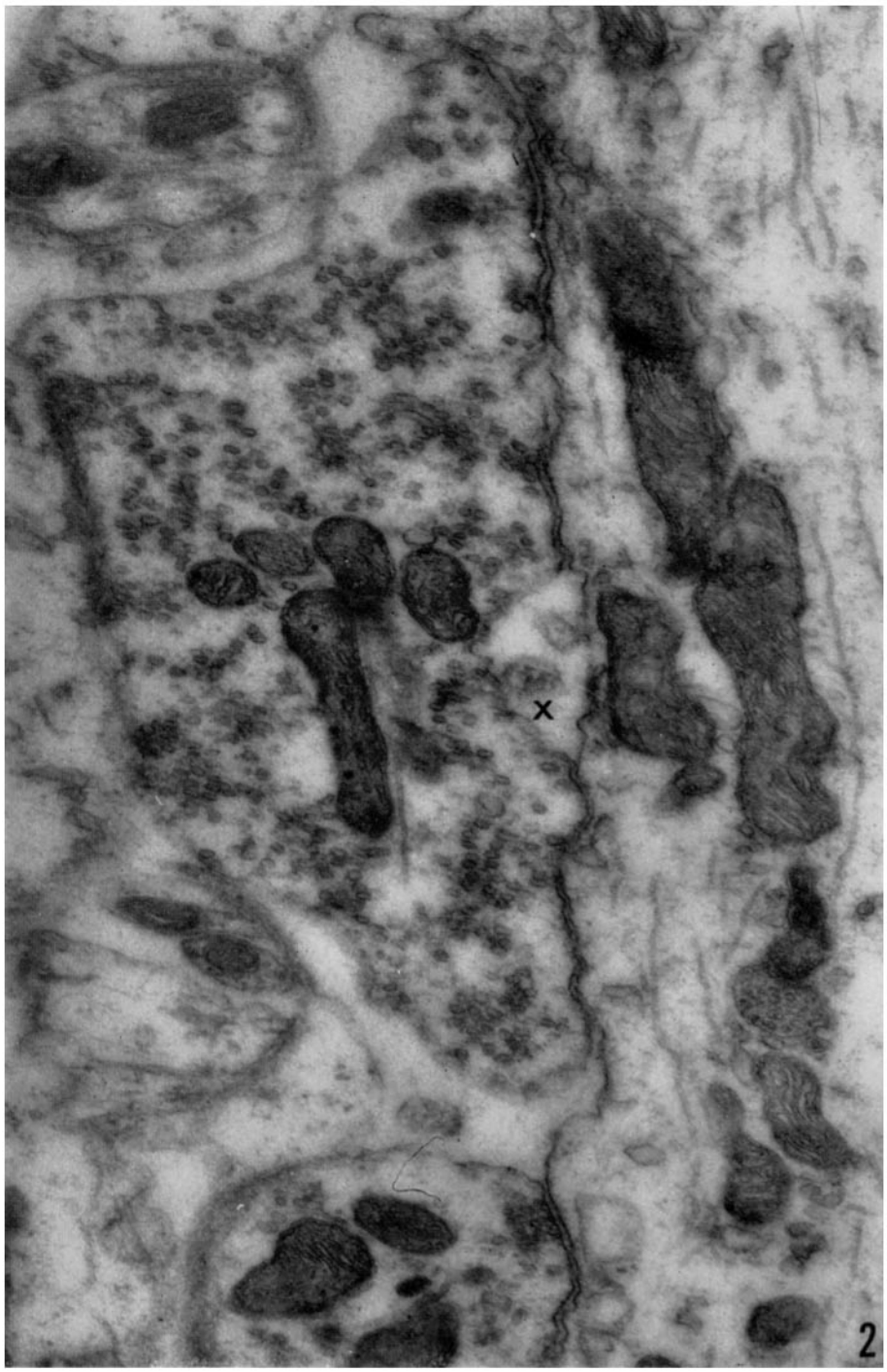
FIG. 1. Electron micrograph of a section through a dendrite and its environs in the abducens nucleus of the rat. Within the dendrite are numerous, more or less parallel, thin, canalicular elements of endoplasmic reticulum displaying occasional vesicular dilatations. Sparse clusters of fine granules correspond to dot-like aggregates of Nissl substance often seen in stained sections of dendrites, particularly at sites of branching. Only a few dendritic mitochondria lie in this field; they are arranged in the peripheral cytoplasm of the dendrite. Attached to the lower surface of the dendrite is one large end-foot ($T_1$) and to the upper surface are three small end-feet ($T_2$, $T_3$, and $T_4$). A telodendron is visible joining the apex of terminal $T_4$. Each ending (except for $T_4$) contains numerous mitochondria and all of them contain clusters of small vesicles, 200 to 650 A in diameter. The base of each ending is separated from the surface of the dendrite by an intrasynaptic cleft approximately 200 A wide. The apposed limiting membranes of the end-feet and dendrite display localized slight thickenings and increased density. × 34,300.




(Palay: Central nervous system synapses)

## PLATE 65

FIG. 2. Electron micrograph of an elongated axon terminal upon a dendrite in the neuropil of the abducens nucleus. The dendrite, containing mitochondria and endoplasmic reticulum, is at the right but is only partly included in the picture. The ending contains mitochondria and numerous synaptic vesicles. To the right of the long mitochondrial profile in the ending is a long, canalicular structure, and a few short ones appear elsewhere in the ending. Notice that many of the mitochondria have longitudinally oriented cristae. The synaptolemma clearly consists of two separate limiting membranes. At *x* the intrasynaptic space is enlarged by withdrawal of the base of the terminal, permitting two glial fibers to pass beween the terminal and the dendrite. × 49,400.

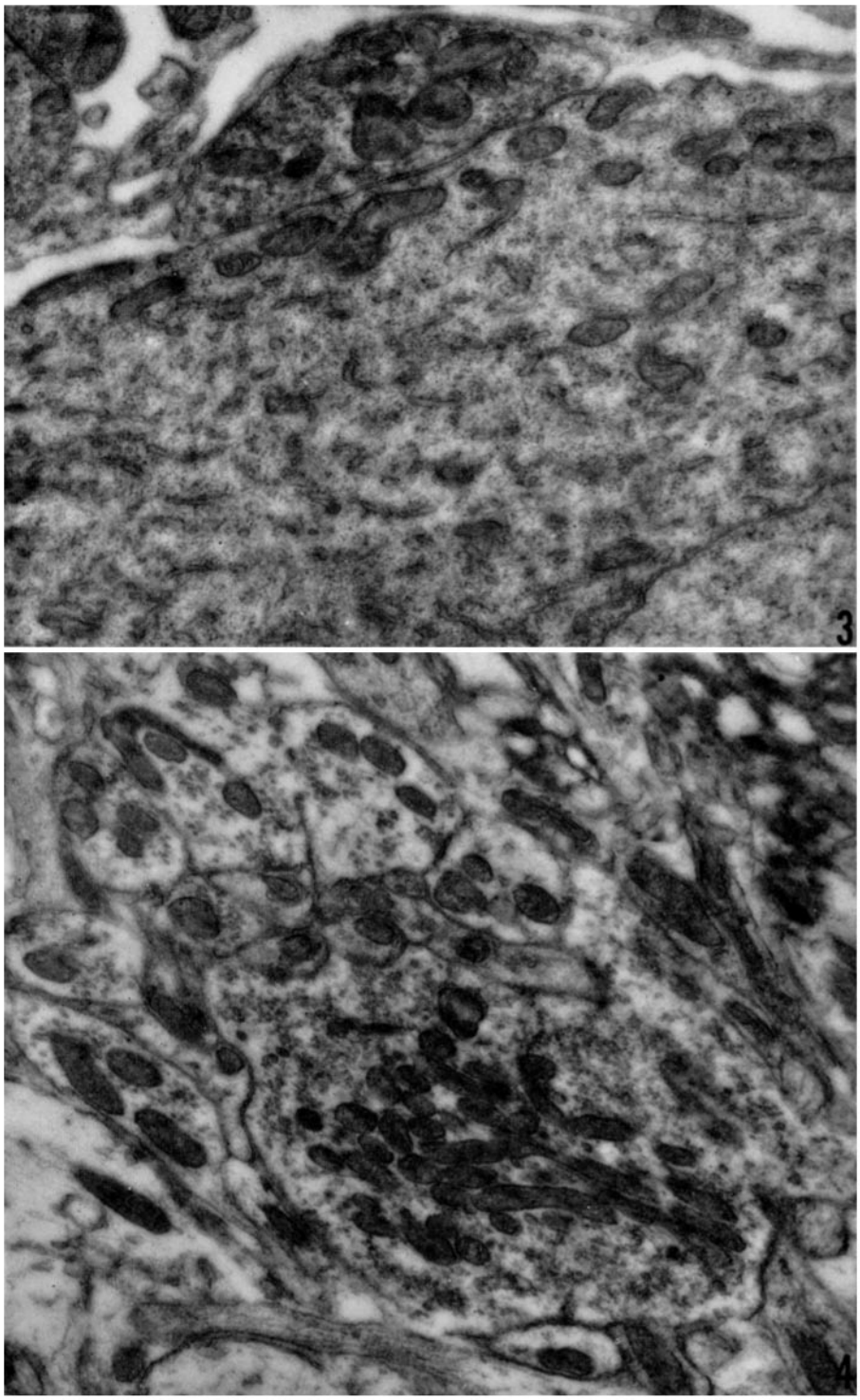



(Palay: Central nervous system synapses)

## PLATE 66

FIG. 3. Electron micrograph showing a portion of a neuron in the dorsal cochlear nucleus. The nucleus of the neuron lies at the lower right bounded by its double membrane. Nissl substance is dispersed throughout the cytoplasm above the nucleus. Close to the surface of the perikaryon is an elongated aggregation of mitochondria. Apposed to the upper margin of the cell is a broad, triangular profile of an axo-somatic synaptic terminal, containing mitochondria and small vesicles. × 28,700.

FIG. 4. Electron micrograph of a section through a glomerulus in the neuropil of the dorsal cochlear nucleus. This complex synaptic apparatus consists of a broad branching axon terminal and associated small dendrites. The axon enters the glomerulus at the right margin of the picture and swells into a rounded branching tip containing a dense collection of mitochondria and small synaptic vesicles. Dendritic tips lie between the main axonal mass and its branches as well as at its lower margin. Glomeruli of similar architecture occur in the granular layer of the cerebellar cortex. × 23,900.




(Palay: Central nervous system synapses)