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ELECTRON MICROSCOPY OF THE INNER PLEXIFORM LAYER OF THE RETINA IN THE CAT AND THE PIGEON

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INTRODUCTION

The inner plexiform layer of the retina is a region of synaptic connexion between nerve cells similar to the neuropil of the central nervous system. It consists of Müller fibres, the processes of the ganglion, bipolar and amacrine cells, and efferent fibres from the optic nerve. The ganglion cell dendrites run diagonally, tangentially or radially, while the processes of the bipolars and amacrines form tangential ramifications from radial trunks (Ramon y Cajal, 1911).

The retina as a whole has a well-defined stratification into cell nucleus and cell process layers. In the mammal this stratification is less evident than in the bird, in which the nuclear layers have separate sublayers for different cell types. The inner nuclear layer in the bird, from the outer plexiform passing inwards, has sublayers for the horizontal cell nuclei, the bipolar cell nuclei, the Müller cell nuclei, and the amacrine cell nuclei (Ramon y Cajal, 1911; Walls, 1942).

In view of these points from light microscopy, it is of interest to attempt to relate the electron microscopical appearances of the inner plexiform layer in the cat and the pigeon to the processes of the various types of cell, especially the amacrine cell. Previous electron microscopy of the retina by Sjöstrand (1949, 1953, 1958, 1959), de Robertis (1956), de Robertis & Franchi (1956), de Robertis & Lasansky (1958), Yasuzumi, Tezuka & Ikada (1958), Ladman (1958), Carasso (1957), and Cohen (1960) has been confined to the pigment, receptor and outer plexiform layers. Villegas (1960) has made observations on all layers of the retina in a mammal (*Macaca*), a bird (*Gallus domesticus*), a reptile, an amphibian and a fish. However, her work does not discuss the synapses in the inner plexiform layer. Ladman (1961) describes the inner limiting membrane of the retina, and Sjöstrand (1960, fig. 5.12) shows a plate of the inner plexiform layer. A preliminary account of some of the results contained in this paper has been published (Kidd, 1961).

MATERIALS AND METHODS

The eyes were removed from cats, anaesthetized with Nembutal, and pigeons, anaesthetized with ether. The eyes were opened and each retina was transferred to a dish of fixative. It was then cut into small pieces by a set of razor blades held 0·5 mm. apart in a clasp (Gray, 1959). Pieces less than 1 mm. in largest dimension were selected for fixation, no attempt being made to select any particular part of the retina. The fixative used was usually 1% osmium tetroxide in Palade-buffered Ringer solution, but on a few occasions a 0·6% solution of $KMnO_4$ in buffered

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Ringer was used. Fixation continued for 4 hr. at 4° C., the tissue was then dehydrated in alcohol, usually stained for 3–6 hr. in 1% alcoholic phosphotungstic acid, and embedded in Araldite (Glauert & Glauert, 1958). $KMnO_4$ produced gross distortion of the inner plexiform layer, but the outer plexiform could be used for electron microscopy. Gold and silver tinted sections were cut with a glass knife on a Porter–Blum microtome, picked up on carbon-coated copper grids, and examined in a Siemens 1*b* electron microscope. Photomicrographs were taken at magnifications of 5000–80,000 and enlarged photographically.

RESULTS

With the exception of the Müller fibres, which frequently can be distinguished from neural processes, electron microscopic criteria for distinguishing the different cell processes in the inner plexiform layer have not been found.

Müller cell processes

These processes contain irregular vesicular or tubular profiles 200–1000 Å. in diameter, filaments 70 Å. in diameter, and granules 200 Å. in diameter. The size of the vesicles and their packing, and the packing of the filaments and granules varies from layer to layer of the retina, and between cat and pigeon.

In the inner plexiform layer of the cat these processes contain few granules, moderate numbers of vesicles, 200–400 Å. in diameter, and some filaments (Pl. 1, fig. 1). The main trunks appear to be about 2μ in diameter, and run radially. It is difficult to identify their many fine side branches in this layer. In the inner plexiform of the pigeon these processes have a very dense cytoplasm containing filaments, but few vesicles (Pl. 1, fig. 2). The trunks run radially and are between 0·2 and 1·5μ in diameter. Their side branches are well adapted to the convex neural processes. Where two Müller cell membranes contact each other they are often only 100 Å. apart (Pl. 1, fig. 2, arrow).

At the vitreal surface of the retina the Müller cells form a continuous layer, covered with a basement membrane (Pl. 1, fig. 3). This is a dense layer 200 Å. thick separated from the free surface of the Müller cells by a less dense layer 300–500 Å. thick. There is a suggestion that both layers contain a meshwork of very fine filaments. In the pigeon, on the vitreal side of the basement membrane, there are some loosely packed 100 Å. filaments (Pl. 1, fig. 4).

Neuronal processes

These can be divided into two types depending on their contents, but a process may show structures characteristic of both types.

(1) Those containing tubules 200 Å. in diameter and of indefinite length, resembling the tubules found in dendrites and some axons by Palay (1956) and Gray (1959). These processes are usually about 0·25–0·5μ in diameter and are infrequent in the inner plexiform layer. In the cat occasional processes, about 1μ in diameter, run tangentially. The tubules are found particularly in radially running processes in the inner nuclear layer of the pigeon (Pl. 1, fig. 5) and frequently where a large process narrows for a short distance (Pl. 1, fig. 6), as found by Gray (1959, 1960).

Cross-sections of tubules can usually be distinguished from vesicles by the greater density of their outlines, and by the smaller variability of their diameter.

(2) Those containing vesicles 200–300 Å. and occasionally up to about 0·1μ in diameter. These processes are the more numerous in both cat and pigeon. They range up to 2μ in diameter and frequently form synaptic contacts with other processes.

Synapses

These are of four kinds.

(1) Conventional synapses. The essential feature of these synapses is the aggregation of 200–400 Å. diameter vesicles against the pre-synaptic membrane (Palay, 1956). These synapses have been divided into two types by Gray (1959). Gray's type 1 is more specialized and shows a widening of the intrasynaptic cleft to 300 Å., as compared with the normal separation between membranes of 200 Å., with a thickening and increased density of the post-synaptic membrane and an intermediate dense line within the cleft (Pl. 2, fig. 7). Gray's type 2 is identified only by the aggregation of vesicles and a slight increase in density of both the apposed membranes. The presence of vesicles in a process without aggregation is not a sufficient criterion for identification of a synapse. In the cat there is a higher proportion of Gray's type 2 than in the pigeon (Pl. 2, fig. 8). The vesicles nearest the pre-synaptic membrane in the type 1 synapse are often much denser than the more distant ones, and scattered densities may be seen between them (Pl. 2, fig. 9, arrows). These densities are so characteristic that it is possible that an arrangement such as that arrowed in Pl. 2. fig. 10 is an obliquely sectioned synapse. Usually the post-synaptic cytoplasm is similar to the pre-synaptic, except for a relative paucity of vesicles and their lack of aggregation.

The conventional type of synapse is the most common in both the cat and the pigeon. Some preliminary counts have been made on a few sections of the inner plexiform layer, and their relative magnitudes confirm the general impression derived from examining many sections. In the cat this type of synapse occurs with a frequency of about 0·2 per μ^2 in thin sections of the inner plexiform layer, and in the pigeon about 0·4 per μ^2. The region of membrane specialization appears, in section, to range up to 0·5μ in length, but is usually much shorter. It is usually much smaller than the region of apposition of the pre- and post-synaptic processes.

(2) 'Spine synapses' (Pl. 2, fig. 10). Compared with the conventional type these are uncommon in both cat and pigeon. Each consists of a post-synaptic process (*sp*) lying in an invagination into a pre-synaptic process (*pre*). The apposed membranes are usually denser over most of their surface and the pre-synaptic membrane is covered with vesicles. Gray (1961) describes this type in the cerebellum.

(3) 'Ribbon synapses'. These synapses are characterized by the presence of a pre-synaptic 'ribbon' (Sjöstrand, 1953), 0·1–0·2μ long and 200–400 Å. wide perpendicular to the pre-synaptic membrane (Pl. 2, fig. 11, *r*). The surrounding cytoplasm contains large numbers of vesicles, which are often aggregated in rows along the ribbon (Pl. 2, fig. 12). The post-synaptic membrane is thickened (Pl. 2, fig. 11, pointers 1, 2), and the intrasynaptic cleft widens to 300 Å. as in the conventional type 1. Often the ribbon synapse is at a corner where three processes meet, the two post-synaptic (post 1, 2) processes having thickened membranes opposite the

ribbon, and the pre-synaptic membrane has a density immediately opposite the end of the ribbon (pointer 3). One of the post-synaptic processes often shows tubules (Pl. 2, fig. 12, *post* 2). Occasionally a ribbon has been found lying parallel to the plane of section, when it appears as an elliptical or rectangular density (Pl. 2, fig. 13, *r*). Two ribbon synapses may be found in the same process, sometimes synapsing with different processes (Pl. 3, fig. 14, *r*1, *r*2). Ribbon synapses are less frequent than the conventional type, occurring about one per $45\mu^2$ in both cat and pigeon.

(4) 'Serial' synapses. The essential feature of such a synapse is a process which is both pre- and post-synaptic. These synapses are of two types, those involving a ribbon synapse (Pl. 3, fig. 14), and those only involving conventional synapses (Pl. 3, fig. 15).

The ribbon type consists of a pre-synaptic process (*pre* in Pl. 3, fig. 14) having a conventional synapse with a process (*b*) which contains ribbons (*r*1, *r*2). This arrangement is uncommon; too few have been seen to estimate their occurrence numerically, but they appear to be as common in the pigeon as the cat.

The second type of 'serial' synapse consists of a process pre-synaptic to a second, which is pre-synaptic to a third. All the synapses involved are of the conventional type, and all three processes have similar cytoplasm except for the arrangement of the vesicles. For example, in Pl. 3, fig. 16, a process (*pre*) synapses with another process (*b*), which synapses with a third process (*post*). Occasionally a more complex arrangement of this type may be seen, as in Pl. 3, fig. 17, where a process (*pre*) synapses directly with a process (*post*), and also appears to connect with it indirectly via a succession of two other processes (*b*1 and *b*2). The conventional type of 'serial' synapse is found very infrequently in the cat, only four have been found by the author, but in the pigeon they occur with a frequency of about one per 300 μ^2.

DISCUSSION

The general appearance of the inner plexiform layer in the electron microscope accords with the findings of previous workers. The cell membranes usually lie about 200 Å. apart, with no large extracellular spaces (Wyckoff & Young, 1956; Palay, 1956, and others), and the cell processes contain mitochondria, filaments, tubules, and vesicles.

The Müller cells have been described by Sjöstrand (1959) in the outer plexiform, and by Villegas (1960) in all layers except the inner limiting membrane, where they have been described by Ladman (1961). The arrangement described here agrees with the findings of these authors except that the 100 Å. separation between cell membranes occurs only occasionally at Müller–Müller contacts and not at Müller-neural contacts. Neither Villegas nor Sjöstrand have described the filaments found in these cells. These increase in their packing density, and the granules decrease correspondingly, from the scleral to the vitreal surface of the retina.

The basement membrane at the vitreal surface of the retina has been described by Ladman (1961). It is similar to basement membranes described elsewhere (Pease, 1958). It appears to vary in thickness, but this is probably due to variation in obliquity of the section. The filaments on the vitreal surface of the pigeon basement membrane may be related to the greater adherence and toughness of the vitreous body in the pigeon.

The criteria for identification of dendrites and axons previously used by Palay (1958), and Gray (1960), cannot be applied to the inner plexiform layer, for several reasons. One is that 200 Å. tubules, usually ascribed to dendrites in the past (though both Palay (1956) and Gray (1960) mention their occasional presence in axons), are found consistently in any process narrowing to less than 0·3 μ, and particularly in all neural processes in the inner nuclear layer, some of which, at least, are axons of bipolar cells. Another reason is the presence of amacrine cell processes, which cannot be identified as either axons or dendrites in Golgi preparations (see below). The final criterion for identification is found at the synapse, assuming that the electron microscopic criteria are established. This work shows that this method of identification too is unreliable in the retina.

Some correlations with Golgi preparations may be made; the main trunks of the Müller cells can be compared directly but, in electron micrographs, their finer branches cannot be identified with certainty in the cat, though they can be in the pigeon. The neural processes are easily confused. Bipolar, ganglion and amacrine cells have radially arranged trunks and tangentially arranged branches. However, unlike the processes of other cells some ganglion cell dendrites run diagonally.

All the cytoplasmic and membrane specializations described here as characteristic of synapses have been noted previously. The conventional kind has been described in the medulla oblongata by Palay (1956), in cerebral cortex by Gray (1959), in the cochlear ganglion by Palay (1958), and in the ciliary ganglion by de Lorenzo (1960). In some of these sites and in the motor end-plate (Robertson, 1956; Reger, 1957), the structure could be related to a known synapse. It has been suggested that the synaptic vesicles carry the quanta of acetylcholine released at the motor end plate (see Castillo & Katz, 1956). The criteria for the recognition of synapses with the electron microscope are sufficiently well established for new deductions to be made independently of the criteria used in light microscopy.

The 'ribbon' type synapse has been described before only in the receptor-bipolar synapse of the retina (Sjöstrand, 1953, 1956; de Robertis, 1956; Carasso, 1957; Ladman, 1958), though Sjöstrand (1960, fig. 5.12) shows a 'serial' ribbon synapse in a plate depicting the inner plexiform layer. The ribbon synapse in the inner plexiform layer appears to differ from that of the outer plexiform layer in the smaller length of the ribbon profile, and its frequent relation to two post-synaptic profiles. The density of the pre-synaptic membrane opposite the end of the ribbon appears to correspond to the 'arciform density' of Ladman (1958). The paired opposed ribbon profiles seen in the rod spherule are not seen in this layer, so presumably the ribbons in the inner plexiform layer are not crescent shaped. They have never been seen to join the cell membrane and, in $KMnO_4$ fixed preparations of the outer plexiform layer, they are of low contrast compared with the cell membrane. They therefore do not seem to be unit membranes but truly intracellular.

Apart from mitochondria and synaptic vesicles, the only intracellular organelles previously described in association with synapses are the synaptic ribbon, the 'spine apparatus' of Gray (1959), and the 'formation sous-synaptique' of Taxi (1961). The last two are post-synaptic and arranged parallel to the synaptic membrane. The ribbon, however, is arranged perpendicular to the pre-synaptic membrane,

and frequently appears in a sharp convexity of the latter. It is not possible at present to suggest a function for any of these structures.

The only structures comparable with the 'serial' ribbon synapses described here are the inter-receptor synapses described by Sjöstrand (1958) in the guinea-pig, but not reported in other species. The 'serial' conventional synapse has not been described elsewhere. It suggests either that the well-documented criteria of a synapse are not applicable to all nervous tissue, or that the inner plexiform layer of the retina has an unusual physiology. This layer certainly differs from other regions of the nervous system in possessing amacrine cells. These cells, or at least the 'amacrines proprement dites' of Cajal, have only processes with the appearance of dendrites in Golgi preparations, though, if dendrites, they conduct excitation in the opposite direction to the bipolars. The fact that 'serial' synapses, though uncommon, are much more numerous in the pigeon than the cat suggests a relation to the high proportion of amacrine cells in the former.

The essential feature of the 'serial' synapse is the process which is both pre- and post-synaptic. Such processes can only be identified when the section passes through at least two synaptic contacts. In random sections this is obviously much less likely to occur than the sectioning of only one of the contacts on a process (when the process would appear to be pre- or post-synaptic) or none (when no deductions on its nature could be made).

It is possible that the 'serial' synapse is the site of an inhibitory process, as suggested by Sjöstrand (1958) for the inter-receptor synapse of the guinea-pig retina. Such inhibition could be of the 'pre-synaptic' type described by Eccles (1961) in the spinal chord. This type does not involve post-synaptic hyper-polarization, but a reduction in the excitatory post-synaptic potential by a depolarization of the pre-synaptic ending. For example, in Pl. 3, fig. 16, process '*b*' might normally excite process '*post*'. However, if process '*pre*' were to depolarize process '*b*' then a spike travelling in process '*b*' would be partially blocked and would have a reduced effect on process '*post*'. 'Serial' synapses have recently been described in the intermediate nucleus of the spinal cord (Gray 1961), the site of pre-synaptic inhibition according to Eccles.

SUMMARY

1. The inner plexiform layer of the retina in cats and pigeons has been examined by electron microscopy. Particular attention was devoted to the synapses of this layer.

2. The retinas were fixed in buffered OsO_4 and stained with alcoholic phosphotungstic acid after dehydration. Araldite was used as the embedding medium.

3. Only the Müller cell process could be positively identified, no distinction being possible between ganglion cell, bipolar and amacrine cell processes.

4. Four main kinds of synapse were identified

(*a*) The conventional kind, similar to those described before in the C.N.S. (*b*) The ribbon type, similar to those described previously in the outer plexiform layer. (*c*) The 'spine' type, consisting of a post-synaptic process invaginating a pre-synaptic process. (*d*) The 'serial' type. This is of two kinds, one being similar to the inter-receptor synapses described previously in the guinea-pig, and a second

kind, not previously described. The latter type involves a process which is post-synaptic to one process and pre-synaptic to another, all the synaptic contacts involved being of the conventional kind.

5. The 'serial' conventional synapse, but not the 'serial' ribbon synapse, is much more common in the pigeon than the cat. It is suggested that this finding may be related to the larger proportion of amacrine cells in the former.

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KEY TO PLATES

b	Process both pre- and post-synaptic	*pre*	Pre-synaptic process
bm	Basement membrane	*r*	Synaptic ribbon
mc	Müller cell	*sp*	Post-synaptic spine
mf	Müller cell filaments	*sv*	Synaptic vesicles
mg	Müller cell granules	*tu*	200 Å. tubules
mv	Müller cell vesicles	*v*	Vitreal space
np	Neural process	*vf*	Filaments in vitreal space
post	Post-synaptic process		

EXPLANATION OF PLATES

Retina of cat or pigeon, OsO_4-fixed and phosphotungstic acid stained. All inner plexiform layer except Figs. 3–5.

PLATE 1

Fig. 1. Cat. Longitudinal section of Müller cell process showing filaments (*mf*), granules (*mg*) and vesicles (*mv*).

Fig. 2. Pigeon. Field showing a group of Müller cell profiles (*mc*), showing some filaments (*mf*). Note 100 Å. separation of Müller cell membranes at arrow.

Fig. 3. Cat. Inner limiting membrane, showing basement membrane (*bm*) and Müller cell filaments (*mf*).

Fig. 4. Pigeon. Inner limiting membrane, showing basement membrane (*bm*), and filaments in vitreal space (*vf*).

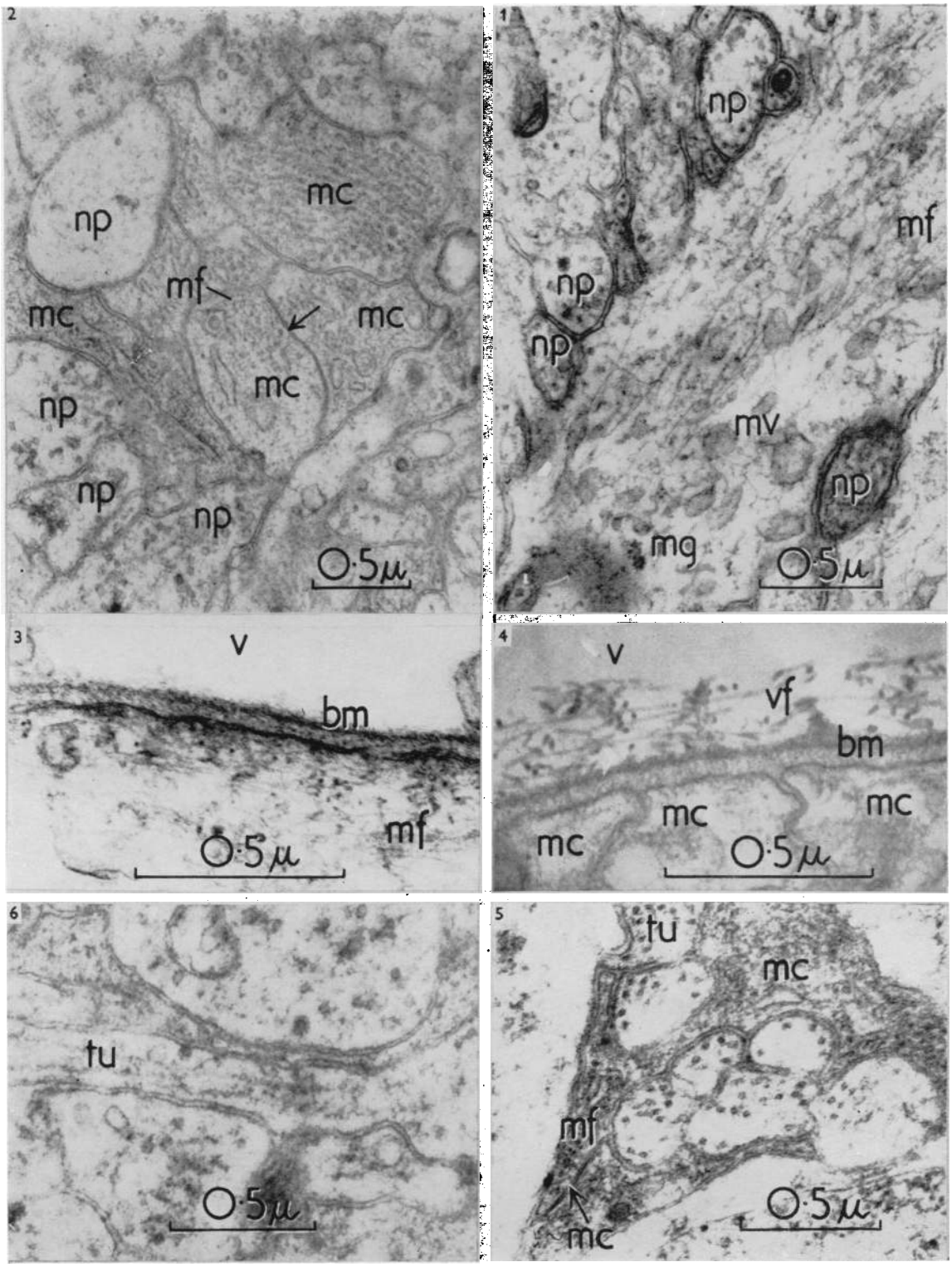
Fig. 5. Pigeon. Section tangential to retina through amacrine cell-body layer of inner nuclear layer. Note processes containing 200 Å. tubules and the density of the Müller cell cytoplasm (containing some filaments in transverse section (*mf*)). Arrow indicates 100 Å. separation of Müller cell membranes.

Fig. 6. Pigeon. 0·2μ process widening to 0·5μ to the right, showing 200 Å. tubules in the narrow part.

PLATE 2

Fig. 7. Pigeon. Conventional synapse (Gray's type 1) showing density of post-synaptic membrane (arrow) and 300 Å. synaptic cleft.

Fig. 8. Cat. Conventional synapse (Gray's type 2) showing density of post-synaptic membrane (arrow) and 200 Å. synaptic cleft.



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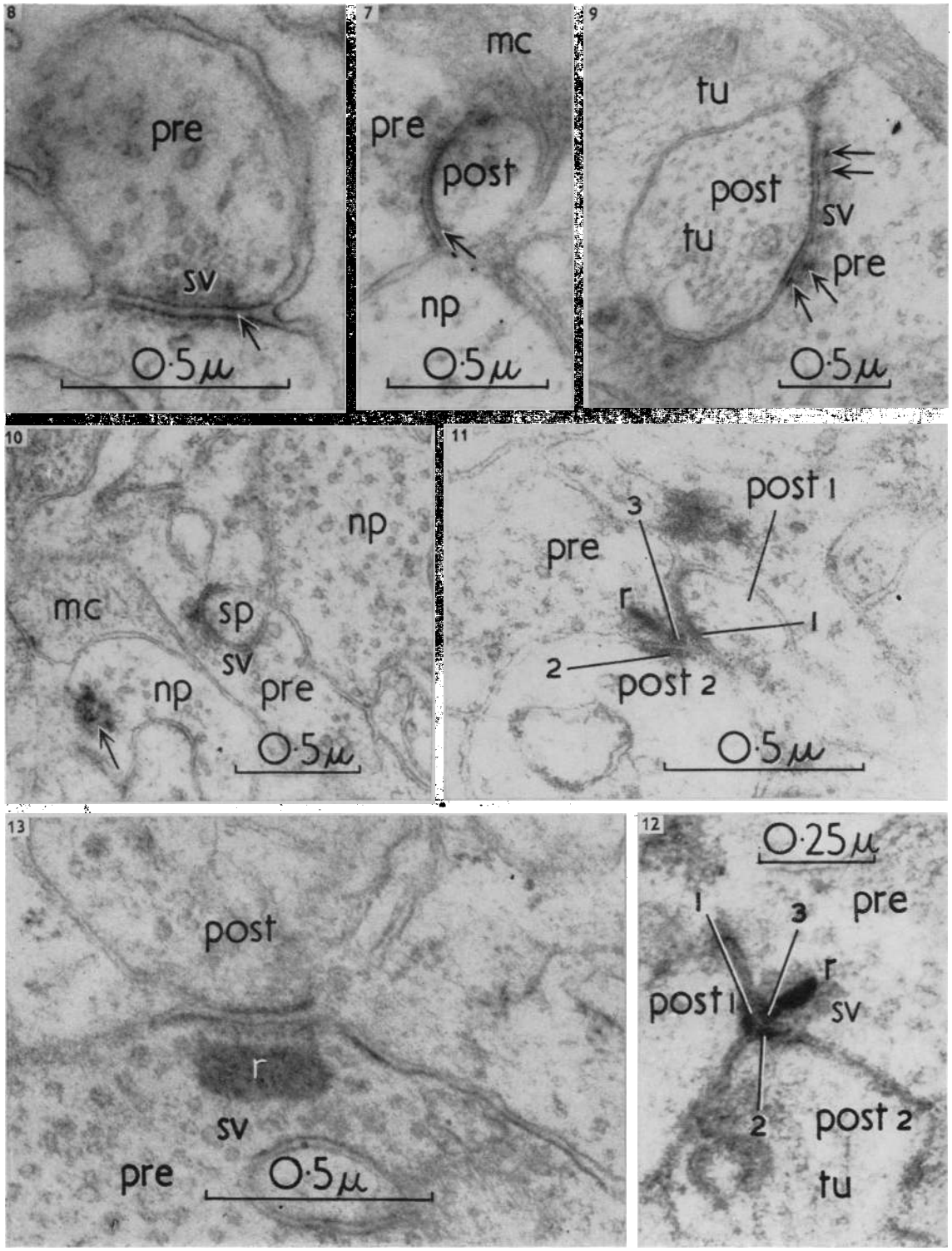
(*Facing p.* 186)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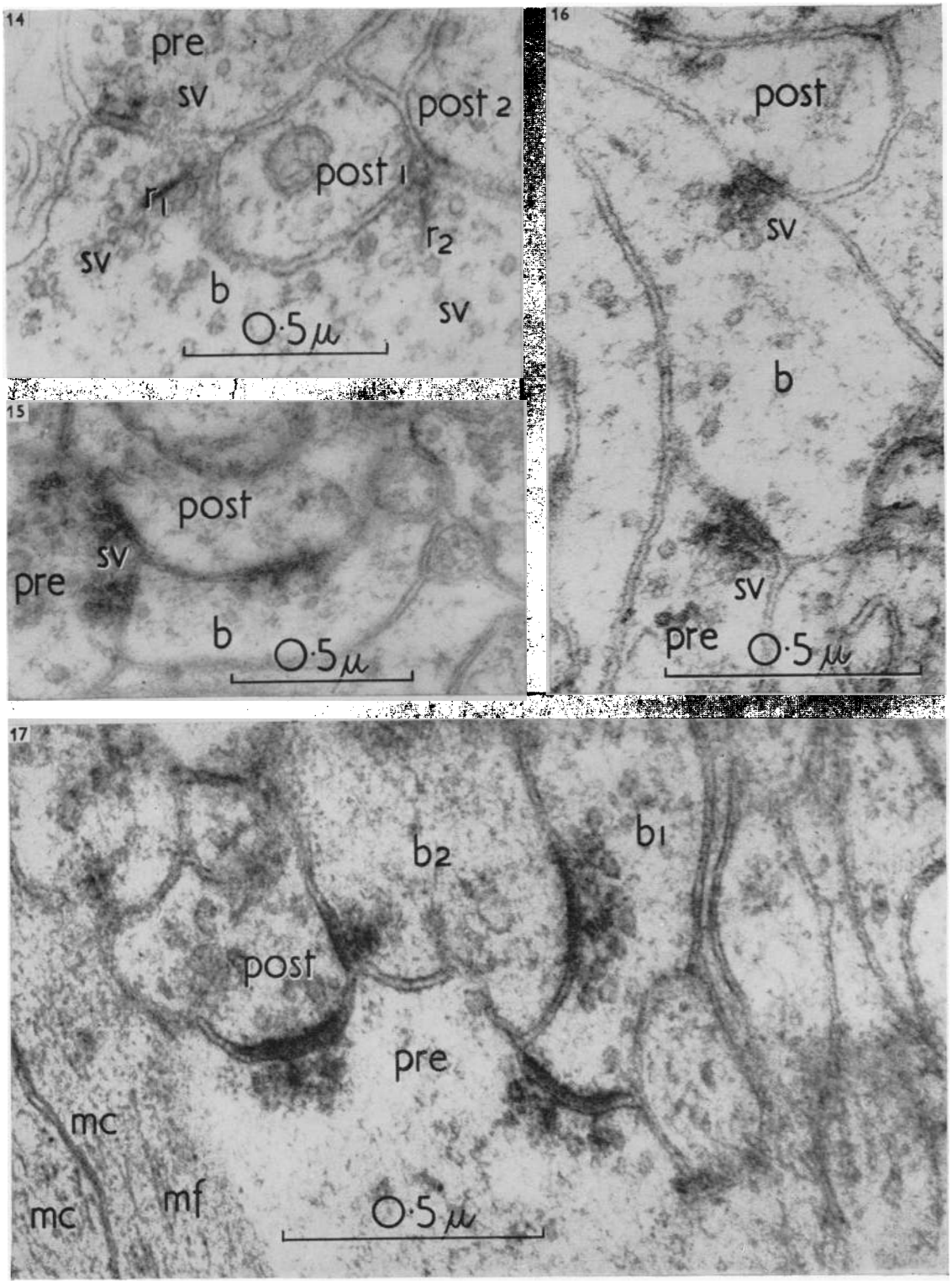
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Fig. 9. Pigeon. Conventional synapse (Gray's type 1), showing density of post-synaptic membrane, 300 Å. cleft, and pre-synaptic vesicles (*sv*) with patchy densities amongst them (arrows).

Fig. 10. Pigeon. Post-synaptic spine (*sp*) obliquely sectioned. Arrowed structure explained in text.

Fig. 11. Pigeon. Ribbon synapse. Pre-synaptic processes (*post* 1, 2). Pointers 1 and 2 indicate post-synaptic densities, and pointer 3 indicates the pre-synaptic density corresponding to the 'arciform density' of Ladman.

Fig. 12. Pigeon. Ribbon synapse with two post-synaptic processes (post 1, 2), the latter showing 200. Å tubules. Pointers 1 and 2 indicate the two post-synaptic membrane densities, and 3 indicates the 'arciform density' homologue.

Fig. 13. Cat. Ribbon synapse showing ribbon (*r*) parallel to the plane of section.

PLATE 3

Fig. 14. Cat. 'Serial' synapse, showing an ordinary synapse on process '*b*', the latter having a ribbon (*r*) synapse with process *post* 1.

Fig. 15. Cat. 'Serial' synapse. Process (*pre*) synapsing with two processes (*post*) and (*b*), '*b*' also being pre-synaptic to process (*post*).

Fig. 16. Pigeon. 'Serial' synapse. Process (*pre*) pre-synaptic to another (*b*), which is pre-synaptic to a third (*post*).

Fig. 17. Pigeon. 'Serial' synapse. Process (*pre*) pre-synaptic to two others, (*post*) and (*b*1), '*b*1' pre-synaptic to a third (*b*2), which is pre-synaptic to a fourth (*post*). The third synapse is identified by the polarity of the membrane densities.