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adopting Sholl's classification, however, is that in electron microscopic preparations, it is far more possible to recognize two main kinds of neuron, and the morphological classes given for pyramidal and stellate neurons in Golgi preparations. So far as the stellate neurons are concerned, some variation in size and cytoplasmic features of perikarya has been encountered in electron microscopic preparations, but an insufficient amount of any one neuron is usually present to enable these variations to be related to neuronal varieties seen in the Golgi preparations.

One of the aims of this study is to distinguish between stellate and pyramidal neurons, and so in addition to describing the morphology of the stellate cells, the manner in which they differ from pyramidal neurons will also be emphasized through-out the text. Only the stellate cells in layers III through V of the rat parietal cortex will be described, since the horizontal cells of layers I and the spindle, or fusiform neurons of layer VI have not yet been examined in detail.

MATERIALS AND METHODS

For electron microscopy, material was taken from the parietal cortex of rats fixed by vascular perfusion with the two side-by-side mixtures suggested by Roesen and Kartenovskv ('67). The first mixture contained 1.25% glutaraldehyde and 1% paraformaldehyde in a 0.05 M cacodylate buffer at pH 7.2. The perfusion was initiated with this solution and then completed with a stronger one containing 3% glutaraldehyde and 4% paraformaldehyde in the same buffer. Both solutions were warmed to 40°C before use and the rat was respirated with a 95% oxygen-5% carbon dioxide mixture until the perfusion was completed.

After fixation, the brain was left in the skull for 24 hours. Next day small pieces of the cerebral cortex were removed and post-fixed to 1% osmium tetroxide in 0.1 M cacodylate buffer. No attempt was made to differentiate between specific cortical areas, but most of the pieces examined corresponded with the description of the cortex as defined by Krieg ('46). When the fixation had been completed, the sections were dehydrated in ethanol and embedded in Araldite. Thin sections were stained with uranyl acetate and lead citrate (Neve and Cougheshall, '63) before examination in an A.E.L. EM 6B electron microscope.

For light microscopy three types of preparations were utilized: thick (1 μm) sections of the above material stained with toluidine blue and pyronine B; thin sections stained with cresyl fast violet and fast blue, and sections of tissue of invented according to the Golgi-Cox modification described by Ramon-Moliner ('01).

OBSERVATIONS

A. Light microscopy

Stellate cells are present in all layers of the rat parietal cortex but they are particularly prominent in layers III, IV and V. Although these neurons have a variety of shapes, all have common features in common. In Golgi preparations they are seen to lack a definite apical dendrite, the cell body is often round or oval and it emerges a number of thin dendrites that have a beaded appearance and are very few, if any, spines (figs. 1, 2). These features enable stellate cells to be distinguished from pyramidal neurons which usually have a prominent apical dendrite that, in common with the other dendrites of this type of cell, bear spines (figs. 2, 3).

In layer IV, and particularly in its lower half, the stellate neurons usually have quite small and round perikarya (40-50 μm in diameter) from which emerge short dendrites that extend in all directions to form an almost spherical field (fig. 1, 2). Generally the dendrites do not arise from thick tapering bases and do not have spines. In most cases, although they are on by no means frequent, some of the frequent dilations, or "beads" that are present along them. Branching of the dendrites is not frequent, and the profuse dendritic tree is not common.

Also in layer IV, as well as in layers III and V, are other stellate cells which are often somewhat larger than the ones described above (figs. 1, 2). The perikarya of these neurons are more oval or pear-shaped, with the long axis, which is about 60-70 μm, oriented at right angles to the surface of the cerebral cortex. Such large stellate neurons have thicker and larger dendrites than the smaller ones and furthermore, although they emerge from all parts of the perikarya, the dendrites are then preferentially oriented in a direction parallel to the layers of the cortex (figs. 5, 6). Many dendrites of these neurons emerge individually from the perikaryon and it is common for groups of two or three of them to arise from the end of a thick common stem (fig. 2). While no axons have been completely impregnated in our preparations, the initial portions of the axons have been apparent. In all stellate cells the axons emerged either directly from the perikaryon, or from the base of one of the dendrites. Often the axons projected towards the surface of the cortex and gave off horizontal collateral branches.

B. Electron microscopy

The main problem was to distinguish between stellate and pyramidal neurons in electron micrographs, and it is appropriate to state briefly how this was accomplished. From classical Golgi studies pyramidal neurons are known to have an apical dendrite that is radial to the cortical surface. Consequently, thin sections were cut at right angles to the surface of the target cells to show the relationship of the apical dendrite emerging from a neuronal perikaryon could be detected. The thin sections were then stained with an electron-dense stain and the perikaryon and cortex and consequently it was possible to locate layer IV, which is the layer in which stellate cells predominate, as the zone deep to the medium and small-sized pyramidal neurons of layers II and III, but above the level of the perikarya of the medium and large pyramidal neurons of layer V. In the parietal cortex this zone is about half-way through the depth of the cortex and is marked by the presence of myelinated nerve fiber tracts oriented parallel to the cortical surface. Neurons were then identified that differed from pyramidal ones in a number of respects, some of which could be correlated with the observations on Golgi impregnated sections. The more obvious differences between these neurons, the stellate cells, and the pyramidal neurons may be summarized as follows:

1. Stellate cells may have dendrites directed towards the cortical surface, but they do not possess in individual one that can be designated as apical.

2. Dendrites of stellate cells are usually thinner than those of pyramidal neurons and contain more closely packed arrays of microtubules. Dendrites lie among their lengths.

3. Dendrites of stellate cells, unlike those of pyramidal neurons, do not bear spines.

4. In layer IV the small stellate cells frequently occur in clusters; the larger stellate cells, however, usually occur singly, as do most pyramidal cells.

5. The perikarya of stellate cells often contain arrays of parallel rough-surfaced cisternae that are frequently arranged to follow the contours of the surface of the nuclear envelope.

6. Particularly in perikarya of larger stellate neurons, the nuclear envelope is frequently ruffled and has an irregular profile.

7. The perikarya of pyramidal neurons bear only one type of synapse that corresponds to the kind designated type 3 by Gray (1959), or symmetric by Colonnier (1968). The perikarya of stellate cells, on the other hand, form this type of synapse, but in addition they have others which have a wider synaptic cleft.

These various features of the stellate neurons, together with other aspects of their ultrastructure, will now be considered in more detail.

1. Cell bodies

The small stellate cells of layer IV frequently occur in groups of three or four (fig. 3), whereas the larger stellate cells of the same and adjacent layers (figs. 4, 5) are generally isolated from each other by intervening neuropl. The nuclei of the small stellate cells tend to be round or oval whereas those of adjacent neurons are relatively evenly disposed, except for small concentrations that occur between adjacent to the nuclear en-
velopes and in the nucleoplasm generally. Nucleoli may also be present in the sections, but these are not distinctive (fig. 5). Overall, the cytoplasm surrounding the nucleus is somewhat darker than that of the proximal pyramidal neurons and this density is produced by the many ribosomes that are contained within it. Some of these ribosomes appear as single particles, but others occur in clumps in rows of the type previously described in other neurons (see Peters, Palay and Webster, 70).

The form of the granular endoplasmic reticulum appears to depend upon the size of the distal cell. In the smaller ones with perikaryal cytoplasm conformed to a thin rim surrounding the nucleus, the cisternae often appear shaper and frequently lie parallel to the surface of the nuclear envelope (fig. 3). In the larger distal cells, however, and in those regions of the perikarya of smaller ones where the cytoplasm forms a thicker layer (fig. 4, 5, 6), many of the cisternae appear in characteristic parallel arrays. Some of the cisternae in these arrays may be quite long and their arrangement is useful in differentiating distal cells from equivalent sized pyramidal neurons, which do not seem to contain such well ordered arrays. The contents of these cisternae are only faintly dense and the ribosomes studied their outer surfaces show areas of closely packed ribosomes separated by intervals of either bare or only have a few individual ribosomes attached to them (fig. 6). These cisternae of granular endoplasmic reticulum, together with the numerous free ribosomes that surround them, constitute the Nissl substance of the cell.

In addition to the arrangements described above, a few cisternae lie in close proximity to the plasma membrane. The side of a cistern lying next to the plasma membrane is usually free of ribosomes and in this region the lumen of cisterns may be dark contents. Such vesicles, the may be occluded so that the inner faces of the apposed cisternal membranes come into close proximity. Such subsurface cisternae sometimes have other ones arranged between them to form regular and closely packed parallel stacks (Roosevelt, 26). In these arrangements, the apposed faces of the stacked cisternae are also bare. Ribosomes only appear on their surfaces if the edges of the stacks, where the cisternae become more widely separated from each other and continuous with the cisternae of the mesaxon, are removed lying deeper in the cytoplasm.

Stacks of closely packed cisternae of the granular endoplasmic reticulum are also sometimes present in the deeper cytoplasm (fig. 8). These resemble the cisternae in the subsurface position, for again, the outer faces of the cisternae are closely apposed, their surfaces are free of ribosomes. In the stacks, ribosomes are present upon the free surfaces of the outer two cisternae, but where a cistern extends away from the stack its surfaces always become studded with ribosomes. In some places the bounding membranes of individual cisternae come together so that their lumens are obliterated (fig. 8).

Like the cisternae of the granular endoplasmic reticulum, those of the Golgi apparatus are most abundant where the perikaryal cytoplasm is thickest. The cisternae generally have quite short profiles and are arranged in closely packed rows with their long axes more or less parallel to the contours of the nuclear envelope (figs. 4, 5, 6). Because they fit together, in electron micrographs these cisternae resemble an echelon of a rough stone wall. At the periphery of the Golgi complex of Golgi cisternae are clouds of vesicular profiles (figs. 6, 7). Most of these vesicles have clear contents like the cisternae, but some are coated or alveolate (Palay, 63; Freytag and Furthauer, 67). These coated vesicles seem to be budded off from the cisternae, for in some places small, nipple-like, coated protrusions project from the surfaces of the cisternae into the surrounding cytoplasm (fig. 6). Other vesicles which are often associated with the Golgi apparatus, but which also occur throughout the cytoplasm generally, have clear contents of which the larger of which may also contain lamellae, are probably lysosomes. These are of varying dimensions. Some are as small as 1,000 A in diameter, while the larger are as large as a small type of mitochondria (fig. 4, 7). Such dark vesicles are more numerous than in the cytoplasm of pyramidal neurons. Multivesicular bodies are frequently found in the outer proximity of the Golgi apparatus, but they also occur elsewhere in the cytoplasm (figs. 7, 12). These vesicles and the flat cisternae are elongated and contain a dark matrix. The cisternae tend to be arranged ellipsoidally across the width of the mitochondria (figs. 5, 6).

Passing between the other organelles are microtubules (200-250 A in diameter) and neurofilaments (90-100 A in diameter). These elongated components of the cytoplasm tend to circumscribe the nucleus (fig. 4) and at the bases of the dendrites and the axon, they converge to enter these processes in parallel array (figs. 4, 7).

Sometimes short, blunt spines 1-2 A long (fig. 6) protrude from the perikarya of distal cells. These are only infrequently encountered, however, and they have not been found in Golgi impregnated distal cells. In one instance in which serial sections were examined, there was no doubt that the protrusion was short and blunt. This spine contained a dense granule embedded dark fluffy material and formed synapses with two axon terminals. In the case of protrusions like the one shown in figure 6, which contains microtubules and membrane bound profiles, the question arises as to whether this is a spine, or the neuronal portion of a longer process such as a thin dendrite. Apparently similar protrusions from the perikarya of stellate cells in the many processes of cells in micrographs published by Colonster (68) and by Lund and Lund (70).

2. Dendrites

As shown in the study of Golgi impregnated distal cells the dendrites of stellate cells radiate from the cell body and within a short distance they assume a relatively uniform thickness (figs. 1, 2). Microtubules from the perikarya funnel into the dendrites and when the ensuing dendrite is thick, a part of the Golgi apparatus usually occupies a central position within the base and extends for some distance into the dendrite itself (fig. 7). In the bases of the thinner dendrites the Golgi apparatus is less abundant and absent. The degree to which the Nissl substance extends into the initial portion of the dendrite also depends upon the thickness of the process. In the thickest dendrites, the extent is such that the character of the cytoplasm in the initial portion of the dendrite resembles that of the perikaryon (fig. 7). But in the thinnest dendrites the Nissl substance diminishes quite abruptly (fig. 4). In longitudinal sections from the proximal portions of dendrites the granular endoplasmic reticulum of the Nissl substance appears as cisternae of various lengths, oriented more or less parallel to the length of the dendrite (figs. 7, 9). These cisternae are frequently located towards the periphery of the dendrite and are particularly prominent in irregular bulges of the dendritic surface. Proximally, the bulges are not prominent, but they become increasingly obvious more distally, where the dendrites are somewhat thinner and show both dilations and constrictions (fig. 10). At the locations of the dilations, the microtubules often kink. These dilations presumably correspond to the ones observed in Golgi impregnated sections, for in electron microscopic material that is not well preserved, it is at the sites of dilations that the inadequate fixation is most obvious, for the cytoplasm becomes vacuolated, the microtubules are more widely separated than elsewhere and tend to bow outwards. Hence, in such material the appearance of the dendrites is more in keeping with what would be expected from a comparison with Golgi impregnated preparations.

In transverse sections of the stellate cell dendrites (fig. 12) the cisternae of the granular endoplasmic reticulum are also quite long and follow the contours of the plasma membrane. Consequently, it can be assumed that most of these cisternae have the form of flattened sheets. Other dendrites (for example see Palay, 64; Peters and Kaiser.com-Abramoff, 70), have a common location where the Nissl substance is well represented in the angle of bifurcation of a dendrite into smaller branches. In contrast with the cisternae of the granular endoplasmic reticulum those of the smooth endoplasmic reticulum (figs. 7, 9, 12) usually have the form of elongated sacs and tubes.

The mitochondria of stellate cell dendrites are longer than those of the perikaryon and lie parallel to the long axis of
the process (figs. 9, 10). As pointed out above, this same orientation is also assumed by the microtubules, which are closely packed and evenly distributed throughout the dendritic cytoplasm (figs. 9, 10, 12). The center to center spacing of the microtubules in stellate cell dendrites is usually of the order of 300-400 Å (fig. 12). This is much closer than the spacing of 2,000-4,000 Å that occurs in the dendrites of pyramidal neurones of the rat cerebral cortex (Peters and Kalinerman-Abramof, '70) and the 1,000 Å spacing in the dendrites of anterior bocca cells (Wuerker and Palay, '69), and is useful in distinguishing stellate cell dendrites from those of the pyramidal cells in the same neurone. In addition, portions of the Nissl substance are more frequently present in stellate cell dendrites. Another important difference is that stellate cell dendrites have never been observed to bear spines.

As will be discussed later, a distinct distinguishing feature is that stellate cell dendrites have very few axon terminals synapsing upon their stumps (figs. 9, 10, 12) whereas the dendrites of pyramidal neurones, have the majority of their synapses upon the spines (see Conradi, '58; Peters; and Kalinerman-Abramof, '70).

3. Axon initial segments

The initial segments of stellate cell axons (fig. 11) have the same features as those of other neurones (for example see Palay, Sotoelo, Peters and Orkand, '68; Peters, Proskauer and Kalinerman-Abramof, '69; Palay, Palay and Webster, '70). At the axon hillock there is a rapid diminution in the amount of Nissl substance present. The axon hillock and these extend into the initial segment, whereas the plasma membrane is characterized by the presence of a distinct underlying coating. The site along the distal portion of the axon initial segment where the axon length loses its underlying coating has not yet been observed. Consequently, whether axonial cell substance, although a few fibrous components are present in the cytoplasm of the initial segment. In addition, microtubules become clustered in the axon hillock and these extend into the initial segment, whereas the plasma membrane is characterized by the presence of a distinct underlying coating. The site along the distal portion of the axon initial segment where the axon length loses its underlying coating has not yet been observed. Consequently, whether axonial cell substance, although a few fibrous components are present in the cytoplasm of the initial segment.

4. Synapses

In this material, synapses have been identified on the basis of the usual criteria (see figs. 4, 5, 6). Namely, that a synapse is an entry formed by two neuronal components whose plasma membranes become apposed to form a junctional complex which often has dense material both in the cleft between the two membranes and applied to their cytoplasmic surfaces. At least one of the neuronal components has synaptic vesicles within its cytoplasm and these accumulate near to the region of the density. In the rat cerebral cortex, only one of the components contains synaptic vesicles and this always seems to be an axon terminal.

Although the perikarya of most stellate cells receive a moderate number of axon terminals (see figs. 4, 5, 6), the perikarya of others receive few (fig. 3). In general, the frequency of synapses seems greatest on the large stellate cells. The proximal portion of the dendrites of stellate cell also receive moderate numbers of synapses (figs. 4, 7, 9) but on the distal portion possibly do not become as concentrated (figs. 10, 12).

On the basis of the width of the synaptic cleft, two main classes of synapse can be recognized on the dendrites and perikarya (figs. 6-7; 9-10). At some synapses, the outer faces of the synaptic clefts are separated by a cleft average 175 Å wide, although some synapses measured with the interior measurements varied between 145 and 210 Å. These measurements only apply to synapses in which the cleft is distinct. Other synapses have a clefts averaging 130 Å wide, but in many cases on synapses, the range is between 110 and 145 Å. Thus in some of the synaptic clefts, the outer faces of the synaptic clefts are essentially identical to the presence of a distinct underlying coating. The site along the distal portion of the axon initial segment where the axon length loses its underlying coating has not yet been observed. Consequently, whether axonial cell substance, although a few fibrous components are present in the cytoplasm of the initial segment.

Particularly on the perikarya the synaptic clefts seem to fall into two categories. One category resembles the form of synapse present upon the dendritic spines of pyramidal neurones (e.g. see figs. 9, 10, 12). Synapses upon the spines of pyramidal neurones are shown in figures 6, 7, 8, 9, 10, and the corresponding synapses upon the perikarya of stellate cells are shown in figures 9 and 11. In these figures it can be seen that such synapses are marked by the presence of a well-defined layer of dense material that is applied to the cytoplasmic face of the postsynaptic membrane and generally, only one such density is present at each synaptic junction. A less prominent and more punctate dense layer is applied to the cytoplasmic face of the preterminal membrane and in the synaptic cleft the dense material is frequently seen to be concentrated towards the middle of the cleft where it forms a plaque about 60 Å thick. Most synapses of this form are made by small axon terminals. In some instances, the same axon terminal may partake in the formation of two synapses, one upon the perikarya or dendrite of a stellate cell and the other on the spine of a pyramidal neuron (fig. 7).

The other category of synapses with wide synaptic clefts is labelled S in figures 11 and 12. These synapses are about from the ones described above in two main regions. The first is that the postsynaptic density on this material is not prominent. The second is that the synaptic junction is long and straight (figs. 6, 13, 14), whereas the synapses with prominent postsynaptic densities tend to have slightly arched and more oblique synaptic junctions (figs. 13, 14). The 7a more difficult to classify. On the perikarya of stellate cells, the synapses with wide clefts and lacking a prominent postsynaptic density from the Nissl substance about from 25% of the synapses with wide clefts. It might be argued that such synapses should not be considered a separate category, these from those with prominent postsynaptic densities, and indeed it must be conceded that the presence of a distinct underlying coating. The site along the distal portion of the axon initial segment where the axon length loses its underlying coating has not yet been observed. Consequently, whether axonial cell substance, although a few fibrous components are present in the cytoplasm of the initial segment.

between the two, particularly when the axon branches of section is somewhat different. Generally, however, when the section plant. Firing of right angles to the synaptic clefts are distinctive in quite apparent. Perhaps the only definite that establish why these two categories of synapses with wide clefts are distinct will be to determine whether they degenerate individually in response to specific deafferentation of the cerebral cortex.

The other class of synapses present on the perikarya of stellate cells, and making contact with about one third of the total, is identical to the form that occurs on the perikarya of pyramidal neurones. On pyramidal perikarya it is the only type of synapse present. The boutons forming these synapses with narrower clefts (figs. 6, 11, 13 and 15) are usually quite large and although the feature is not marked in the present material, a few of the synaptic vesicles have elongated profiles (figs. 13, 15). The synaptic complexes are usually quite short (figs. 13, 15) and more than one may be present at the same interface between the axon terminal and a perikarya. By synaptic complex is meant an assemblage of synaptic vesicles together with the associated junctional density (see Palay, '58, and Peters, Palay and Webster, '70). Associated with the synaptic complexes are puncta adhaerentia (Peters, Palay and Webster, '70). These are junctional zones which have no associated concentration of synaptic vesicles and are marked by prominent cytoplasmic densities that are symmetrically distributed.

It must be made clear that not all synapses can be readily put into one of the above categories, and an example of such a synapse is shown in figure 14. The upper synapse, labelled S, clearly has the characteristics of one with a wide and straight cleft, but lacking a prominent postsynaptic density. The lower synapse, unlabelled, is more difficult to classify. On the perikarya of the stellate cell, the synapses with wide clefts and lacking a prominent postsynaptic density. In some instances, the same axon terminal may partake in the formation of two synapses, one upon the perikarya or dendrite of a stellate cell and the other on the spine of a pyramidal neuron (fig. 7).

The other category of synapses with wide synaptic clefts is labelled S in figures 11 and 12. These synapses are about from the ones described above in two main regions. The first is that the postsynaptic density on this material is not prominent. The second is that the synaptic junction is long and straight (figs. 6, 13, 14), whereas the synapses with prominent postsynaptic densities tend to have slightly arched and more oblique synaptic junctions (figs. 13, 14). The 7a more difficult to classify. On the perikarya of stellate cells, the synapses with wide clefts and lacking a prominent postsynaptic density from the Nissl substance about from 25% of the synapses with wide clefts. It might be argued that such synapses should not be considered a separate category, these from those with prominent postsynaptic densities, and indeed it must be conceded that the presence of a distinct underlying coating. The site along the distal portion of the axon initial segment where the axon length loses its underlying coating has not yet been observed. Consequently, whether axonial cell substance, although a few fibrous components are present in the cytoplasm of the initial segment.
imimately the same proportion as upon the perikarya. As a dendrite extends further from the cell body however, the synapses with narrow clefts and those with wide clefts but lacking a prominent postsynaptic density become increasingly less common. Consequently, upon the smaller dendritic branches the synapses with wide clefts and a prominent postsynaptic density predominate (Figs. 9, 10, 12). These usually occur in large numbers and in longitudinal sections of small dendrites, their postsynaptic densities are conspicuous (Fig. 10), providing a ready means of identifying stellate cell dendrites and distinguishing them from the dendrites of pyramidal neurons. These latter bear most of their synapses upon spines (Peters and Kaiserman-Abramof, 1970) and very few occur upon the stems of the dendrites. The close packing of synapses that may occur upon the dendrites of stellate cells is also evident on figure 15. In this example, three axon terminals are adjacent to each other, while a fourth one is on the outer side of the dendrite. Although not always the case, the remainder of the dendritic surface is covered with the processes of protoplasmic astrocytes.

Each of the three basic forms of synapses occur close to the axon hillock of stellate cells, but on the axon hillock itself the synapses with narrow clefts and small synaptic complexes predominates. In one example shown in figure 11, an axon terminal (A), seems to form such a synapse on the axon hillock and on its other face forms a synapse with a wide cleft upon a dendritic spine of a pyramidal cell. However, this arrangement is not common. An insufficient number of initial axon segments have been encountered to draw definite conclusions about the synapses that occur upon their surfaces, but all of the cases that have been observed have been of the type with narrow clefts and slight synaptic complexes.

DISCUSSION

From the above description, it is apparent that the stellate cells in the rat cerebral cortex have a morphology sufficiently different from that of pyramidal neurons for profiles of parts of these two types of neurons to be distinguished from each other. The only prominent feature of the definite structure of stellate, or non-pyramidal, cells appear to be these made by Colonnier and Roche (1969), and by Lund and Lund (1970). Colonnier (1969) gave a brief account of the stellate cells in layers I and IV of the visual cortex of the cat, while Lund and Lund (1970) described the salient features of the stellate cells in the paraventral cortex of the rat. In general, their descriptions agree with the one given here. In each instance, the circular or oval outline of the cell body is mentioned as well as the observation that the cytoplasm of these cells tends to be denser than that of pyramidal neurons. As shown here, this density can be attributed to the greater concentration of free ribosomes in the cytoplasm of stellate cells. Additionally, Colonnier (1969) and Lund and Lund (1970) also report that the dendrites of stellate cells do not bear spines.

In the present account, use of the terminology suggested by Gray (1956) and by Colonnier (1968) to describe the forms of synapses in the cerebral cortex has been avoided. Gray (1956) suggested that in situ fixed by osmic acid, synapses are of four types: Type I synapses occur on the dendritic spines and smaller dendrites, Type II synapses occur on dendritic trunks and the perikarya of neurons. Type I synapses are recognized by having a cleft which is 150-200Å wide and a prominent accumulation of dense material on the cytoplasmic face of the postsynaptic membrane. Type II synapses have a narrower cleft and the postsynaptic density is less apparent. Colonnier (1968) found that Gray's classification was somewhat inadequate, and suggested that the term 'axo-dendritic' should be used to describe a synapse in which the postsynaptic density is continuous with the synapse. Colonnier and Roche (1969) on the other hand, distinguished between the two types of synapses in the visual cortex of the cat.

There is little information about the effects of preparative techniques upon the character of the synapse, although preliminary observations have shown that the synapses of stellate cells may be relatively unaffected by the processes of postmortem fixation. The number of specimens used is too small to allow any conclusion, but it is interesting to note that axo-dendritic synapses are not altered by these procedures, while axo-axonic synapses may be lost.

Acknowledgments

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LITERATURE CITED


PLATE 1

EXPLANATION OF FIGURES

1-2 Cold preparations of the middle layers of parietal cortex. Stellate cells with round (S) and oval (O) cell bodies are shown. The latter have dendrites that tend to be oriented in a vertical direction. In contrast to those of pyramidal neurons (P), stellate cell dendrites lack spines and are beaded. X 300.
PLATE 2

EXPLANATION OF FIGURE

A group of three small stellate cells from layer IV. The nuclei (N-N₁) of these cells are surrounded by a thin rim of cytoplasm. Granular endoplasmic reticulum (ER) is well developed only where the cytoplasm is most abundant. One neuron has a dendrite (D) emerging from the perikaryon and another, the initial segment of the axon (A₁-A₂). Axon terminals making synapses with these three neurons are indicated by arrows. X 3,000.
PLATE 3
EXPLANATION OF FIGURE

4 A large stellate cell from layer IV. This neuron has a rounded nucleus (N) which is surrounded by a perinuclear reticulum made up of numerous endoplasmic reticulum (ER) arranged to form small Nissl bodies. The Golgi apparatus (G) is apparent and passing between the expansions are axons of microglia. Note the smooth-surfaced dendrite (D) emerging from the cell body and the manner in which the Nissl substance diminishes at its base. The base of a second dendrite (D2) is also labelled. Axon terminals synapsing with the surface of this neuron are indicated by arrows. ×9,000.
PLATE 4

EXPLANATION OF FIGURE

5 The cell body of a large stellate neuron. The nucleus (N) of this neuron contains a prominent nucleolus (Ne) and is bounded by a rather ruffled nuclear envelope. Granular endoplasmic reticulum (ER) is present in the perikaryon and is particularly prominent at one pole, where it forms a peculiar, dense, The golgi apparatus (G) is also prominent in this region. Notice the large number of free ribosomes and the groups of lysosomes (L) in the cytoplasm. The positions of axons terminals forming synapses with this neuron are indicated by arrows. X 15,000.
Part of the cell body of a large stellate cell. On the left is the nucleus (N) which is bounded by a ruffled nuclear envelope. In the surrounding cytoplasm are many profiles of cisternae of granular endoplasmic reticulum (ER) with its irregular meshing of ribosomes. Many clusters of ribosomes lie free in the cytoplasm. Associated with the Golgi apparatus (G) are numerous vesicles. Some of these are coated and appear to bud off from the Golgi cisternae (arrows). A spine (sp) projects from the surface of the neuron and at its tip it forms a synapse with an axon terminal (A). Unlike the spines of pyramidal cell dendrites (dp), this spine contains microtubules and a mild vacuolar body. A number of axon terminals (Ae-Af) synapse with the surface of the neuron. These synapses are of three types: (1) Synapses (Hi) with wide clefts and a prominent postsynaptic density, which are similar to the synapses on the spines (sp) of pyramidal neurones; (2) Straight synapses (Hg) with wide clefts and little postsynaptic density; and (3) Synapses with narrow clefts and short synaptic cisterns (Hh). See later figures for other examples of synapses of these three types. × 25,000.
PLATE 6
EXPLANATION OF FIGURES

7 Proximal portion of a dendrite from a large stellate cell. At the base of the dendrite is part of the Golgi apparatus (G1), and this extends for some distance distally (G2), as does part of the Nissl substance (N) which tends to occupy a position close to the plasma membrane. Associated with the Golgi apparatus are multivesicular bodies (mvb). Other membrane-bound components of the cytoplasm are vesicles, some with dense contents, and microtubules. Microtubules (m) pass between these other organelles. These dendrites have smooth surfaces and lack the spines (sp) that typify pyramidal neurons. Associated with the stellate cell dendrites are four axon terminals (A–A'), three of which are forming synapses (Sb, Sa, and Sb'), Synapse Sb' has a wide cleft and little associated density. Synapse Sb has a narrow cleft, and although the structure of synapse Sa is not clear, the density indicates it to be of the type with a wide cleft and a prominent postsynaptic density. Unlike the other axon terminals, Sa consists of a number of dark vesicles. × 30,000.

8 Portion of stellate cell cytoplasm containing a group of parallel cisternae of the granular endoplasmic reticulum. These cisternae are closely opposed and in two places their lamellas are obliterated (arrows). Ribosomes stud only the outer facing of the two bounding cisternae, although other ribosomes occur where the cisternae leave the edges of the group. Below these granular cisternae is part of the Golgi apparatus (G2). × 30,000.
9 Longitudinal section of a stellate cell dendrite close to the cell body. Compared to the proximal portion of a dendrite shown in figure 7, the cytoplasm of this more distal portion shows a diminution in the amount of granular endoplasmic reticulum (ER) which is confined to a few dispersed cisternae. Microtubules (MT) pervade the cytoplasm, although a few cisternae of smooth endoplasmic reticulum (SR) are present both beneath the plasma membrane and between the microtubules. In this micrograph all of the axon terminals (A) form synapses (S') with wide clefts and well developed postsynaptic densities. This same type of synapse is also present on the spine (sp) of a pyramidal neuron. X 30,000.

10 Longitudinal section of a small dendritic branch of a stellate neuron. With the exception of a few mitochondria, the cytoplasm is occupied by microtubules. Not the dilations along the dendrite and the many synapses (arrows) formed on its surface. X 10,000.
PLATE 8
EXPLANATION OF FIGURES

11. On the left of this micrograph is the axon hillock of a stellate cell and extending to the right is the initial axon segment. The initial segment has an undercoating (a) and the microtubules (mt) are arranged in clusters. Few ribonuclei (r) are present in the initial segment. On this part of the neuron, the axon terminals (A₁, A₂, A₃) form synapses with narrow clefts and late postsynaptic densities. Compare these synapses with the ones present on the spine of a pyramidal cell spine (sp) and note that one axon terminal (A₄) is forming synapses both on a spine (sp₁) and the axon of the stellate cell. x 28,000.

12. Transverse section of two stellate cell dendrites (D and D₂). The larger dendrite (D) is probably sectioned close to the cell body, because it contains long profiles of granular endoplasmic reticulum (ER) in addition to mitochondria (mit), a profile of the smooth endoplasmic reticulum (ER) and a multivesicular body (mvb). The microtubules are less obvious than those in the smaller dendritic profiles (D₂). All of the axon terminals (A₁) surrounding the large dendrite (D) form synapses (s₁) with prominent postsynaptic densities. Between the axon terminals are processes of astrocytes (A₁). A similar synapse (A₁) is also present on the cell body of the stellate cell that occupies the lower portion of the figure. x 35,000.
PLATE 9
EXPLANATION OF FIGURES

13 Portion of the perikaryon of a stellate cell which is forming synapses (S₁ and S₂) with three axon terminals (A₁, A₂ and A₃). One synapse (S₁) has a vesicular junction with a wide cleft and little postsynaptic density. The other two synapses (S₂) have short complexes and narrow clefts. Note the synapse on the nearby dendritic spine (sp). × 33,000.

14 Two axon terminals (A₁ and A₃) synapsing on the surface of the perikaryon of a stellate cell. One axon terminal (A₁) forms a synapse (S₁) with a straight junction, wide cleft and little postsynaptic density. The other terminal (A₃) forms a junction with a short synaptic complex (arrow) and a punctum adhaerens (p). Note the wide synaptic cleft. This micrograph is an enlargement of part of figure 6. × 60,000.
PLATE 10

EXPLANATION OF FIGURES

15 Two synapses on the perikaryon of a stellate cell. One synapse (S) has a wide cleft and a prominent postsynaptic density. The other synapse is formed by a large axon terminal and has only a short synaptic complex (S). Note the astrocytic processes (As) surrounding the axon terminals. × 60,000.

16 An axon terminal (A) forming two synapses (S). One synapse is on the spine of a pyramidal cell dendrite and the other on the cell body of a stellate cell (N). × 70,000.