Combined Golgi and Electron Microscopic Study on the Synapses Formed by Double Bouquet Cells in the Visual Cortex of the Cat and Monkey

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ABSTRACT The morphology of certain Golgi-stained cells was examined in the striate and peristriate cortex of the cat and in the striate cortex of the rhesus monkey. Neurons in layer III were selected on the basis of their characteristic vertical axon bundles, which are 20–150 μm in diameter and traverse layers II–V. Selected neurons were examined under the electron microscope to characterize their synapses and to establish their postsynaptic targets. It was found that double bouquet cells form symmetrical or type II synapses. In the cat the postsynaptic membrane specialization was more extensive than in the monkey. After removing the Golgi precipitate from boutons of two cells in the cat, small pleomorphic and flattened vesicles were found in the boutons. Earlier suggestions that double bouquet cells make synapses preferentially with spines of apical dendrites could not be confirmed. Out of 47 boutons in area 17 of the cat, 88.4% formed synapses with dendritic shafts, many of them belonging to nonpyramidal cells; 9% with perikarya of nonpyramidal cells, and only 2.6% with spines. Out of 19 synapses examined in area 15, 74% were contacting dendritic shafts and the rest contacted spines. In the monkey 60% of a total of 38 double bouquet cell synapses made synapses with dendritic shafts. A different type of double bouquet cell with densely spiny dendrites is also described in layer IV of the monkey striate cortex. This neuron formed asymmetrical synapses.

It is suggested that layer III double bouquet cells with vertical axon bundles are probably inhibitory and act on other nonpyramidal cells and certain parts of pyramidal cells.

One of the most interesting yet poorly understood cortical local circuit interneurons is Ramón y Cajal’s "cellule à double bouquet dendritique," first described in various cortical areas from man (Ramón y Cajal, ’11) and subsequently found in the sensory cortex of the cat (Szentagothai, ’73) and monkey (Jones, ’75) and in the visual cortex of the monkey (Szentagothai, ’75; Valverde, ’75; Valverde described these neurons in area 18 of the monkey but did not find them in the striate cortex (Valverde, ’75), nor were they mentioned in another Golgi study (Lund, ’73). Although the cell is called “double bouquet” or “double tufted” after its dendritic arborization, a far more characteristic and unique feature of this cell is its narrow, columnar axon bundle passing radially through several layers.

Previous Golgi studies (Ramón y Cajal, ’11; Colonnier, ’66; Jones, ’73; Szentagothai, ’75, ’78) agree in describing the vertical axon bundles of double bouquet cells as following apical dendrites, which are known to receive asymmetrical or type-I synapses on their spines (LeVay, ’73; Fransen et al., ’77; Sonnygi, ’78). The idea that the axon bundles provide the synapses on the apical dendrites is based on the respective courses of apical dendrites and the tight fascicles of the double bouquet cells. However, the Golgi method, though successful in revealing individual neurons, has obvious limitations in identifying

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synaptic connections at the light microscopic level. Recently efforts have been made at the electron microscopic level to trace synaptic connections of cortical neurons characterized by Golgi staining (de Lasey, '79). Painet et al., '77; Parnavelas et al., '77; Somogyi, '77, '78, White, '78; Peters et al., '79). This approach has been very informative in attributing the post synaptic structures to different types of local circuit neurons (Somogyi, '77, '78, White, Peters and Falckén, '78; Somogyi et al., '79).

In the present study we have used the Golgi method to characterize double bouquet cells in striate and peri striate areas of the cat and in the striate cortex of the Macaque Monkey. Selected cells were processed subsequently for electron microscopy to identify the type of synapses formed by double bouquet cells. We also sought to determine the nature of post synaptic structures and the types of post synaptic cell types.

MATERIALS AND METHODS

Two normal adult cats and two adult monkeys (Macaca mulata) were used. In both monkeys an electrolytic lesion was made in the left lateral geniculate nucleus 4 days before death and for reasons unconnected with the present experiment. The cells described in the present study were in the striate cortex ipsilateral to the lesion, but it was not the aim of the present study to trace degenerating boutons to these cells. Following a lethal intravenous injection of 1% Nembutal (Naflural) the animals were perfused through the heart with 0.9% saline, followed by an aldehyde mixture containing 20% paraformaldehyde and 36% gluteraldehyde in 0.1 M sodium phosphate buffer at pH 7.4. After 20 minutes continuous perfusion the skull was opened and small blocks of the cortex were dissected and placed in the same fixative for 3-4 hours, or overnight, at 4°C. Thereafter the blocks were processed for Golgi staining and electron microscopy essentially as described previously (Somogyi, '78). Some of the blocks, however, were fixed in 2% OsO₄ instead of 2% as used previously. Some of the Golgi sections were rinsed in 96% etha in for 5-5 minutes before dehydration. This partially removed the silver chromate precipitate from the most superficial structures in the section and thereby uncovered some of the internal detail within the impregnated elements, although the extent and depth of silver chromate removal varies from section to section and is difficult to control, it was possible to examine two cells in this way in area 17 of the cat.

Cells were drawn using a 100 x oil immersion objective and a Leitz camera lucida. In the monkey drawings were made of one cell in layer III and two cells in layer IV complete with their impregnated axons. In the cat, one cell in area 17 and four cells in area 17 with their axons, and two further cells in area 17 without their axons, were also drawn and photographed. All were in layer III. All quantitative data given relate to the Golgi sections. No correction was made for shrinkage. In the monkey the layering scheme of Lund ('78) was used.

Some of the cells (Table 1) were reexamined for electron microscopy. To improve contrast for electron microscopy Golgi sections were stained with uranyl acetate and lead citrate and ultrathin sections were cut with lead citrate as described previously (Somogyi, '78). Electron micrographs were taken on Philips 201 and EM400 electron microscopes using 20 µm objective apertures.

RESULTS

Light microscopy of Golgi-stained double bouquet cells in layer III

Cells in layer III were selected on the basis of their vertical axon bundle descending through layers III-V in addition to the dendritic morphology. Nonpyramidal cells with very different dendritic organizations may possess similar dendritic arborizations. Light and electron pericellular cells and cells with radial axon bundles were found throughout this layer (Figs. 2, 3, 18) except its most ventral part (Fig. 4). The poor density of granule cells and sparsely thorny dendrites originate from the upper and lower plexuses (Fig. 18). These regions of the axon and superficial layer in V and especially in layer III, and as a result the axon field increases in these layers (Figs. 3, 15).

In the monkey striate cortex the radial fibers always form small fascicles of 20-50 µm in diameter (Figs. 14, 16). They have more swellings and fewer side branches. The number of branchings decreases as the fibers travel toward the bottom of layer IV where the radial fibers terminate and give off a few short collaterals (Figs. 15, 18). In both species the thick axon fascicles produce very high bouton density per tissue volume (Figs. 3, 15).

Electron microscopy of Golgi-stained double bouquet cells

The Golgi-stained axonal collaterals were followed in electron microscopic serial sections for five structural characterization of the synapses and to identify the post synaptic structures. It has been extensively demonstrated in two previous papers (Somogyi, '78, Somogy et al., '79) that with our method any stained bouton can be correctly identified and recovered for electron microscopy; therefore, to save space the light and electron microscopic correlation is shown only in one example (Fig. 4). The synapses formed by the impregnated double bouquet cells were compared on electron micrographs to synapses established by unstained boutons with the same post synaptic structure (Figs. 3, 6, 7, 17, 18) as well as with synapses formed in the same area in the cat (Figs. 3, 12, 15).

In the cat the radial fibers descend to layers II and III and descend to upper layer V (Figs. 2, 3, 16). They may course in a loose plexus 100-150 µm in diameter (Figs. 2) or of the collaterals may form small fascicles in which case the entire bundle is only 20-50 µm in diameter (Figs. 1, 4, 13). The main radial collaterals have swellings throughout their length and bear small branches crowded with bulbous enlargements (Figs. 1, 2'/4, 3/4, 13). These branches are most numerous in layer V and especially in layer III and as a result the axonal field increases in these layers (Figs. 2, 16).

In the monkey striate cortex the radial fibers always form small fascicles of 20-50 µm in diameter (Figs. 15, 16). They have more swellings and fewer side branches. The number of branchings decreases as the fibers travel toward the bottom of layer IV where the radial fibers terminate and give off a few short collaterals (Figs. 15, 16). In both species the thick axon fascicles produce very high bouton density per tissue volume (Figs. 15, 18).

Electron microscopy of Golgi-stained double bouquet cells

The Golgi-stained axonal collaterals were followed in electron microscopic serial sections for five structural characterization of the synapses and to identify the post synaptic structures.
The boutons contained flattened or small pleomorphic vesicles (Figs. 10–12) with occasional large dense-core vesicles also present. This corresponds well to the vesicle types in unstained boutons in the same material, where symmetrical membrane specialization and pleomorphic vesicles are found together (Fig. 3).

**Electron microscopy of postsynaptic structures**

The nature and distribution of postsynaptic structures is summarized in Table 1. It can be seen that there is a difference between the two species and also between areas 17 and 18 in the cat. However, in view of the small number of cells examined and the large variance within the group of three cells in area 17 of the cat it is not our intention to attach any special significance to these differences.

In areas 17 of the cat 86.4% of the boutons terminated on small and medium size dendritic shafts (Figs. 4B–D, 6, 7, 10, 11, 12A) which have no particular orientation. Some of these dendrites were followed in long section series but no spines could be detected on their surface. Many (64%) of the postsynaptic dendrites received synapses from one or more non-impregnated synaptic boutons in the same section which included the impregnated bouton (Figs. 6, 7). The majority of nonimpregnated boutons established asymmetrical contacts. Main shafts of pyramidal cell apical dendrites were not encountered among the postsynaptic dendrites. Six axosomatic synapses (Figs. 5, 8) were identified between the Golgi-stained boutons and four nonpyramidal neurons, three of which were fusiform with dendrites originating from the upper and lower poles of the perikaryon. One of the synapses was in fact on the emerging main shaft, but was classified as axosomatic (Fig. 5). These neurons could be identified as being nonpyramidal since they received both asymmetrical and symmetrical synapses from unstained boutons on their perikaryon (Colonnier, VB. Fernández et al., 77).

No pyramidal cell perikaryon or axon initial segment was ever found among the postsynaptic structures. The origin of the three spines postsynaptic to the stained neurons in area 17 of the cat could not be determined.

One neuron was studied under the electron microscope in area 18 (Figs. 13, 14). Synapses were more frequently 26% bound postsynaptic to the axon of this neuron (Fig. 14A) but the majority of the synapses were still established with dendritic shafts. One of these shafts could be an apical dendrite since it had a radial course and was about 2 mm in diameter. It received only symmetrical synapses on
the shaft and two spines receiving asymmetrical
synapses were seen to emerge from its
surface. Another shaft in synaptic contact
with an impregnated bouton emitted two
spines, both of which received asymmetrical
synapses (Fig. 14B). The other dendrites were
small or medium size without particular orien-
tation. Only a small number of unstained
boutons were found to terminate on the postsynaptic dendrites, indicating that some of
them are different from those in area 17.
Synapses were seen only in four cases in the
plane of the impregnated bouton.

One layer III double bouquet neuron in the
monkey striate cortex was reprocessed for
electron microscopy. Many more spines were
found to be postsynaptic to this neuron than
in the cat (Table 1). The proportion of spines
was somewhat greater in layer III than in
layer IV. All these spines received one asym-
mmetrical synapse from boutons containing
round synaptic vesicles (Fig. 17A) in addition
to the symmetrical synapse established with
the impregnated bouton. The spines had very
long but thin stalks which made it impossible
to trace back to the parent dendrites. Postsyn-
aptic dendritic shafts (Fig. 17B, C) were small
to medium diameter and 19% of them were in
asymmetrical synaptic contact with non-
impregnated boutons (Fig. 17C). They had no
particular orientation.

We were particularly interested to see
whether one postsynaptic structure receives
multiple synapses from one double bouquet
cell. In each species two reconstructions were
made from serial sections. It was found that
neighboring or closely situated boutons usu-
ally form synapses with different structures.
Two neighboring synapses on the same den-
drite were only occasionally observed (Fig. 6).
However, two of the postsynaptic perikaryons
received two adjacent synapses from a double
bouquet cell.

Layer IV spiny double bouquet cells in the
monkey

The lack of specific synaptic relationship
between apical dendrites of pyramidal cells
and the axons of double bouquet cells found in
layer III leaves the question of the origin of
presynaptic boutons on apical dendritic spines
open.

Double bouquet cells have also been de-
scribed in layer IV (Shinomiya, 73, 74). There-
fore we thoroughly studied this layer,
but so far have failed to find similar cells to
those in layer III. However, we encountered a
new type of small spiny cell with a remarkably
narrow vertical dendritic field (Figs. 18, 19).
The fusiform perikaryon was about 7-10 μm
in diameter and was always in layer IV. The
radial dendrites formed two narrow col-

![Image of synaptic structure](image-url)

**Fig. 4.** (A) Photomontage of part of the vertical spin bundle of the neuron shown in Figure 1. A boxed area is shown
at the electron microscopical level in (B). Structures remain to A and B are a neuron (N), a glial cell (G), the Golgi-stained
collateral (a), and a Golgi-stained bouton (b). Small collateral. The bouton is shown at higher magnification (C) forming a synapse (arrow) with a dendritic shaft (D). The other bouton (b) is seen three-sections away at the largest
extension of the synaptic contact (arrow). Scales = A: 50 μm; B: 7 μm; C and D: 0.2 μm.
Fig. 5. A and B, Serial sections of a nonglycine-ergic (NG) which received two synapses from the Golgi-stained cortex in Figure 1. In addition to the impregnated bouton described in Figs. 6 and 7, the faintly stained cell body is shown at higher magnification where the impregnated bouton makes a type I synaptic contact (arrow). Note the more extensive postsynaptic density of the type I contact in (C).

Fig. 6. Two boutons of the same axon collateral from the same neuron of the cell in Figure 1 make type II synapses (arrows) with a nonglycine-ergic cell dendrite (d), which also receives three type I synapses from boutons containing spherical vesicles (asterisks). Scale = 0.5 μm.

Fig. 7. A dendrite shaft (d) containing a lamellar body (lb) receives a type II synapse (arrow) from the bouton of the cell in Figure 1 and a type I synapse from a bouton with spherical vesicles (asterisks). Scale = 0.2 μm.

Fig. 8. Asymmetric synapse (arrow) established by the impregnated bouton of the cell in Figure 1 with the perikaryon of a nonglycine-ergic cell. Scale = 0.2 μm.

Fig. 9. Demonstration of the terminal arborization plaque (open arrow) between the impregnated bouton and a dendrite (d) with dense material accumulation on both sides. Scale = 0.2 μm.
Fig. 10-12. Gally-impranated boutons of double bouquet cells. The Golgi precipitate was partially removed from the boutons. Scales = 1.2 μm.

Fig. 13. Drawing of a cell with vertical axon bundle in layer II of area 18 in the cat's lateral gyrus. The axon is only partially drawn, as indicated with a horizontal line in A and B. Scale and labelling as in Figure. See electron microscopic data in Table 1.

Fig. 10. (A,B) Serial sections of an axosomatic synapse (large arrow) established by neuron No. 2 in Table 1. Note flattened synaptic vesicles (white arrow) and an electron-dense line in the synaptic cleft.

Fig. 11. A cluster of pleomorphic vesicles (white arrows) in a bouton of the same cell as in Figure 10. The bouton makes a synapse (arrow) with a dendritic shaft (d).

Fig. 12. (A,B) Two boutons of neuron No. 3 in Table 1. (A) One bouton contains small pleomorphic vesicles and establishes a type II synapse (arrow) with a dendrite (d). Two other boutons (asterisks) containing larger vesicles establish type I synapses with spines (S). (B) Small pleomorphic vesicles are revealed in a bouton of the same neuron after removal of the Golgi precipitate. Scales = 0.2 μm.
Fig. 14. (A) Type II synapse established by the cell in Figure 13 with the head of a spine (S). In (B) a dendrite (d) ending a spine (S) receives a synaptic contact from the impregnated bundle of the afferent cell. Because of the tangential section, the synaptic cleft is not seen here. Another spine (S₂) was traced in vertical sections of the same dendrite. (B) Spine received synaptic contact from bundle containing round vesicles. Scale = 2 μm.

Fig. 15. Drawing of Golgi-impregnated cell (R) with vertical axon bundle (A) in the striate cortex of the monkey. The axon bundle has been separated into three parts which should be continuous at the points marked by broken lines at X, Y, and Y'. Arrow indicates the afferent bundle. The position of the nucleus in the cortex is shown in C. See electron microscopy data in Table 1. Scales = A and B: 50 μm; C: 100 μm.
Fig. 16. Photograph of part of the cortical axon bundle of the cell shown in Figure 15. Scale = 20 μm.

Fig. 17. Details from the same plateau seen in Figure 16 are shown to make type II synapses (arrows) with a spine (A) and with dendritic shafts (B and C). The spine and the shaft in C receive a type I synapse from a bundle containing several synaptically related terminals. Scale = 0.2 μm.

Fig. 18. Drawing of two spiny double bouquet cells in layer IV of the striate cortex of the monkey. The area outlined is indicated by an arrow. The positions of the cells are shown in C. Cell B was studied under the electron microscope (see Table 1), and two of its collaterals were found to become myelinated (B). Scale = A and B, 50 μm; C, 100 μm.
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Intrinsically about 20-50 μm in diameter, descending and ascending in layers IVb-C. They branch once or twice but the branches preserve a radial direction. The largest dendrites may terminate in a small tuft. Shortly after leaving the soma, the dendrites become encrusted with typical long-stalked spines (Fig. 18, 19).

The axon usually originates from the lower pole of the perikaryon, taking a descending course, and emits several recurrent collaterals. As far as we have been able to reveal only small parts of the axonal field. One reason for this, as later electron-microscopic studies showed, is that many of the collaterals become myelinated.

None of the boutons of the ingrown part of the axon were studied under the electron microscope (Table 1). All made asymmetrical synaptic contacts with pronounced postsynaptic membrane specializations. Spines (Fig. 20A) and dendritic shafts (Fig. 20B) were the postsynaptic elements, the latter being more numerous.

DISCUSSION

The neurons described in layer III of rat or monkey are identical to Ramón y Cajal’s “cellules à double bouquet dendritiques” (Ramón y Cajal, 1911, Figs. 345, 348, 351), to some of the “cells with horse-tail shape axons” described by Szentágothai (1973, 1975, Szentágothai and Aratbh, 1976), and to Valverde’s “cells with tight vertical bundles” (Valverde, 1978). It is surprising how the description given by Jones (1975) of cells in the monkey somatosensory cortex exactly reproduces the features of cells found in our study in different cortical areas and in different species, which may indicate the ubiquitous role played by these neurons in cortical circuitry.

The naming of cortical neurons is a matter of varying clarification (Mann, 1979). The essential difference between neuron classes is the difference in input and output. As efforts to characterize the afferent and efferent connections of identified cortical neurons started only recently (LeVay, 1972; Kelly and Van Essen, 1974; Somogyi, 1977, 1978; Percheron et al., 1977; Fairén et al., 1977a, 1978a, 1978b; Peters and Fairén, 1978; Peters et al., 1978; Gilbert and Wiesel, 1979; Lin et al., 1979), the data do not allow a comprehensive consideration. Consequently, classifications based either on light microscopic single neuron staining, such as the Golgi method, or on purely electron microscopic analysis remain in use. To avoid introducing yet another term in the present study we frequently use the name “double bouquet dendritic neuron” coined by Ramón y Cajal. It must be emphasized, however, that other neurons with totally different afferent inputs may have similar double bouquet dendritic fields. Fusiform neurons with similar smooth or sparsely spiny dendrites have been described in layer III of the visual cortex of the rat, but their axons form specialized terminal bouton rows synapsing on the axon initial segment of pyramidal cells (Somogyi, 1977).

In the present study another double bouquet cell was described in layer IV of the monkey’s striate cortex. Although possessing a narrow dendritic cylinder like that of the layer III cells, it differed sharply from the latter by having densely spiny dendrites and making asymmetrical synaptic contacts. This means that its connections are different from the layer III cells, yet it is properly described as a double bouquet cell. This neuron is probably a variety of spiny stellate cell, since the latter also form asymmetrical synaptic contacts (LeVay, 1972; Somogyi, 1978; Somogyi and Cowley, unpublished observations in the monkey).

The relatively small number of described synapses established by this cell type does not yet allow the characterization of the postsynaptic neuron. The nine identified synaptic contacts do not indicate the involvement of apical dendrites among the postsynaptic structures. Previous Golgi studies (Valverde, 1972; Szentágothai, 1978, Lund, 1977) on the monkey striate cortex no similar neuron was described, which shows the limitations of this method in sampling neuronal populations.

As the dendritic morphology is not entirely unique to the neuron type the vertical axon bundle was used as an additional criterion in this study, and the synapses and postsynaptic structures were also characterized to obtain information on the connectivity of the neurons.

Interest has been focused on this type of neuron because its morphology is well suited to distributing information in the vertical direction through layers II-IV. This idea fits well with the results of physiological studies demonstrating a laminar organization of the visual (Hubel and Wiesel, 1972) as well as other cortical areas (Mountcastle, 1977; Assenmacher, 1979 in which the initial input is confined predominantly to layer IV and is distributed by local circuit interneurons to other layers in a narrow column. Such a scheme is supported by proposals that the vertical axon bundles of layer III double bouquet cells ter-

Fig. 19. Photomicrograph of neuron B in Figure 18. White arrow indicates the axon hillock. Distance of the cell labelled by arrows is shown in Figure 20. Scale = 30 μm.

Fig. 20. Asymmetrical and type 1 synapses (arrow) formed by the Golgi-stained horizontal labelled in Figure 19. In (A) the synapse is on a spine (S) and in (B) it is on a dendritic shaft (D). Scale = 5.0 μm.
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minute on the bases of apical dendrites (Ra-
mön y Caja, 11: Colonial, 69; Sandegedahl,
73, 75, 78). This proposal could not be con-
formed in the present study. In neiter species were apices of spines of dendrites a major factor in the diameter of double bouquet cells. On the basis of this fact, it was not possible to determine whether the apical dendrites could be the post synaptic target. Whether a cell exerts mainly inhibitory or excitatory action through its synapses is not possible to determine by morphological meth-
ods. However, there is converging evidence that in the cerebral cortex at least some of the neurons which form symmetrical synapses and contain pleomorphic vesicles are inhibitory. Glycine acid decarboxylase, the synthesizing enzyme of 3-aminobutyric acid (GABA), has been localized in these boutons in the cortices of both rat (Ribak, 78) and monkey (Ribak et al. 79). Furthermore, there is increasing evi-
dence that GABA is an inhibitory transmitter in the cerebral cortex (Iversen et al. 71; Rose and Blackman, 74; Sillito, 76; Iversen et al., 79). It is even more pertinent to the present study that motor cells have vertical dendrites which have been shown to contain glutam-
ic acid decarboxylase (Ribak, 78) and ac-
ccurately localized in layer III (see Emans and Lindvall, 79). This indicates that glutamic acid decarboxylase does not prove that GABA is a transmitter in the brain, but rather it is possible in the neurons desc wide in layer III of the monkey cortex that the synapses of the cells which with their axons, perhaps through a method which makes it possible to localise intracel-
lular HRP in cells post synaptic to the cerebellum in the cortex (Somogyi and Palay, 72). Some of the dendrites shafts post synaptic to the double bouquet cells could be the basal dendrites of pyramidal cells or the symmetrical dendrites of the pyramid cell axon initial segment in the soma. It is known that each synapse with an axon shaft has a site for the axons, as in the present study. The Golgi staining, or diffuse, can be observed. Compared to symmetrical asymmetrically oriented or ascentral cell bodies are significantly symmetrical. In two cases the ratio of the diameter of these dendrites, very likely of pyramidal cell origin, is equal to the target. Spines which in layer III probably measure 1.8 times their diameter in layer III, the majority is the portion of spine was greater than the adjacent neuron number increased in layer III, where the majority can be shown to be possessed by the cat, certain parts of pyramidal cells also contain a number of the descending dendrites of double bouquet cells. It is difficult to assess whether the differ-
cence in the postsynaptic structures between the two species and between the two cortices of the cat are significant. The number of boutons studied is not sufficient for

a thorough statistical analysis. Nevertheless for the two most extensively studied neurons in area 17, the difference between the cat and the monkey is not very striking and the efferent synaptic relationships of these particular neurons in the two species. This implies that the inhibitory innervation is extrapo-
led from one species to another when synaptic relationships of morphologically similar neurons are concerned. The idea of apical dendrites being the post-
synaptic target of double bouquet cells has been attacked because it seemed to explain the narrow, strictly radial course of the axon. It suggested a climbing type of interaction. This could not be confirmed in the present study since the radial banded axons do not seem to follow any particular postsynaptic structure. Multiple synapses on the same dendrite were rarely observed. However, since the vertical axon plexus has a high density target it is likely that the axon of one double bouquet cell encounters the dendrites or perikarya of the same postsynaptic neuron several times. Instead of the climbing type of connection these factors could also explain the small diameter of the axon cylinder. If one thinks of not one neuron but ensembles in double bouquet cells with vertical axon bundles, these axons form a dense "cerebral cortex" and the distribution of a single neuron would be extremely sharp because of the small lateral spread of the axon. Such axial as-
semble spread of an axon from the cerebral cortex to motor nuclei can be demonstrated in the activity of neighboring neuron popula-
tions in a stable fennessee. Cortical neurons of the monkey cortex have been shown to have smooth or sparsely spiny dendrites and have been studied to establish the site of the apical dendrites (Rakic and Fon) have shown that the majority of the neurons in layer III (78) have reported sixth neurons in the rat stratum which established synapses with prominent axons. In the present study (78) have found the majority of neurons in layer III which form symmetrical synaptic terminals. This pyramidal cell perikarya, axonal segments, apical dendrites and somas were found among the postsynaptic structures. In contrast, dendritic terminals on terminal sites another local circuit interneurons, the axon collateral, was found to form synaptic, the axon, as well as the soma of pyramidal neurons in the rat, cat, and monkey (Somogyi, 77, 79). Somogyi, 77). This neuron forms synapses with the soma of pyramidal cells and with cells of high degree of specificity with regard to the post synaptic target, which is not significant for the functional layer III double bouquet cell, whose overall specificity is unsurpassed among known cortical local circuit inter-
neurons. The latter neurons are not found in the monkey but in the cat the axon bundles occupy a narrow cylinder between layers I and V. Regionally, the postsynaptic structures of these neurons are not ab-
solutely specific but: neither pyramidal cell nor axon initial segment were found among the 120 synapses examined so far and an apical dendrite shaft was possibly found in only one case. This clearly shows selectivity and preference for certain postsyn-
aptic elements and emphasizes yet again the intricate wiring of the cerebral cortex.

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Monosynaptic Cortical Input and Local Axon Collaterals of Identified Striatonigral Neurons. A Light and Electron Microscopic Study Using the Golgi-Peroxidase Transport-Degeneration Procedure

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ABSTRACT
Following the injection of horseradish peroxidase into the ipsilateral substantia nigra, 36 retrogradely labelled neurons in the striatum were characterized (in three rats) by Golgi staining and gold toning; each neuron was of the medium- or large-spiny type. Prior to the injection of horseradish peroxidase, two of the rats had had lesions placed in the ipsilateral motor cortex, the third rat had had a lesion placed in the ipsilateral frontal and prefrontal cortex. In the electron microscope, degenerating boutons of cortical neurons were found in asymmetrical synaptic contact with the spines of proximal and distal dendrites of all six of the identified striatonigral neurons that were studied. Some of the degenerating boutons were small (diameter 0.1-0.3 μm), while others were larger (1-2 μm). An individual dendrite of a striatonigral neuron was in synaptic contact with very few degenerating boutons.

Local axon collaterals in the striatum could be traced from two of the identified striatonigral neurons that received degenerating cortical boutons. These were studied in the electron microscope; their boutons formed symmetrical synaptic contacts with spines or dendritic shafts of other striatal neurons. The synaptic boutons contained, large, clear, round or pleomorphic vesicles. The postsynaptic targets of these boutons morphologically resembled the dendrites of medium-size spiny neurons.

It is concluded that afferrors from the cortex make monosynaptic contact with the dendrites of medium-size spiny striatonigral neurons and that such neurons have local axon collaterals in the striatum that form symposis with other spiny neurons.

The mammalian neostriatum receives its main afferrors from the cerebral cortex, from the thalamus, and from certain cell groups in the mesencephalon (for references see Carpenter, 76; Grosovsky, 79; Nauta and De Morsier, 79). The cortical projection is topographically organized, and apparently the whole neocortex sends fibres to the neostriatum (White and Nauta, 65; Webster, 61, 65; Kemp and Powell, 70). However, the projection does not show a simple point-to-point topology, since more than one cortical region may project to the same region of the striatum in a discontinuous fashion, and the area of the projection is not related to the dimensions of the cortical area (Kemp and Powell, 70; Goldman and Nauta, 77; Garcia-Rill et al., 79; Veening et al., 80).

The way in which the neostriatum integrates and transforms information arriving from the cortex (or other nuclei) before passing it on to the pallidum and substantia nigra is poorly understood, largely because we know so little

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