Exp Brain Res (1984) 53: 295–303

Experimental Brain Research


# Characterization by Golgi Impregnation of Neurons that Accumulate $^3$H-GABA in the Visual Cortex of Monkey*

P. Somogyi[1], Z.F. Kisvárday, T.F. Freund, and A. Cowey

1st Dept. of Anatomy, Semmelweis University Medical School, Tüzoltó u. 58, H-1450 Budapest, Hungary
Dept. of Experimental Psychology, Oxford University, South Parks Road, Oxford OX1 3UD, UK

**Summary.** $^3$H-GABA was injected into restricted regions of visual areas 1 and 2 (cortical areas 17 and 18) on the lateral surface of the occipital lobe in monkeys. The injected tissue was processed for Golgi impregnation and gold toning. Sections containing Golgi-impregnated neurons were re-embedded, sectioned at 1 μm, and prepared for autoradiography to reveal neurones that had selectively accumulated $^3$H-GABA.

Golgi-impregnated pyramidal, spiny stellate and aspiny nonpyramidal neurons were examined for $^3$H-GABA accumulation. Out of 47 aspiny nonpyramidal neurons 16 were labelled by $^3$H-GABA. The other cell types did not accumulate the amino acid. Twelve of the labelled neurons were drawn. Eight were bitufted neurons with their dendrites oriented predominantly radially, three were small multipolar neurons, and one could be reconstructed only partially. One neuron had a locally arborizing axon in layer III.

Two bitufted, Golgi-impregnated neurons in layer II and upper III of area 18 were labelled from GABA injection radially beneath in layer VI, providing evidence for earlier suggestions that in the monkey's visual cortex the cells in the upper layers which project radially and accumulate $^3$H-GABA are aspiny non-pyramidal cells. The results indicate the existence of different types of putative GABA-ergic interneurons.

* During part of this project P. Somogyi was supported by the Wellcome Trust at the Department of Pharmacology, Oxford University. We are grateful to the Hungarian Academy of Sciences, the International Cultural Institute of Budapest, the Wellcome Trust, the Royal Society, the E.P. Abraham Cephalosporin Trust, and the Medical Research Council for financial support

1 Present address: The Flinders University of South Australia, School of Medicine, Dept. of Human Physiology, Bedford Park, South Australia 5042

*Offprint requests to:* Dr. P. Somogyi (address see footnote 1)

**Key words:** GABA uptake – Golgi impregnation – Interneurons – Inhibition – Monkey visual cortex

## Introduction

In the visual cortex γ-aminobutyric acid (GABA) is probably an inhibitory neurotransmitter (Krnjevic and Schwarz 1967; see also Emson and Lindwall 1979; Iversen et al. 1971). In the visual cortex of monkeys neurons which presumably use GABA as their transmitter have been localized by immunocytochemical demonstration of the GABA-synthesising enzyme glutamic acid decarboxylase, GAD (Hendrickson et al. 1981), and by autoradiographic localization of exogenously applied $^3$H-GABA (Somogyi et al. 1981a, 1983a). In the autoradiographic studies a specific pattern of interlaminar connections was revealed by means of $^3$H-GABA injections that were largely confined to a single lamina in any particular vertical section through the cortex. However, little is known about the types of neuron responsible for these interlaminar connections because autoradiography reveals only the perikaryon of the labelled neuron and immunocytochemical studies of GAD at present reveal only the perikaryon and proximal dendrites together with isolated boutons whose parent cell body is impossible to identify. In our previous study fine structural criteria were used to identify neurons in layers II and III as non-pyramidal cells projecting vertically down to layers V and VI (Somogyi et al. 1981a). Further information about the types of neuron accumulating $^3$H-GABA can be obtained by combining autoradiography with Golgi impregnation of the labelled neuron (Somogyi et al. 1981b; Bolam et al. 1983; Somogyi et al. 1983b). In the present study various types of Golgi impregnated

neuron were examined by autoradiography for the selective accumulation of $^3$H-GABA following its injection into different laminae of areas 17 and 18 of monkeys. Some of the results have been presented in preliminary form (Cowey et al. 1981).

## Methods

One rhesus monkey, *Macaca mulatta*, and two cynomolgus monkeys, *Macaca fascicularis*, were used. Two were previously used in behavioural experiments and had received surgical section of the central third of the corpus callosum and the underlying fornix 6 months earlier. The other had a high antibody titre to Herpes simiae and could therefore be used only in short-term experiments. There was no reason to suppose that the occipital cortex was abnormal. Animals were sedated with i.m. injection of 10 mg/kg of ketamine hydrochloride (Ketalar, Parke-Davis) and deeply anaesthetized i.v. with sodium pentabarbitone (Sagatal, May and Baker). After removing the bone over the lateral occipital lobe and opening the dura the occipital cortex was injected with $^3$H-GABA (0.33 mM, 55–60 Ci mmol$^{-1}$, Radiochemical Centre) dissolved in Krebs bicarbonate as described earlier (Somogyi et al. 1981a, b; 1983a, b). Injections were delivered through glass micropipettes penetrating at a very oblique angle to the surface of the cortex, thus ensuring that the injection track travelled in the same cortical layer for a considerable distance. The capillary was advanced for 6–8 mm and then gradually withdrawn in 0.5–1.0 mm steps while 0.05–0.1 μl of $^3$H-GABA was injected by pressure at each step. A total of 8–10 μCi was delivered along one injection track. Every injection was made parallel to the lunate sulcus and from medial to lateral in occipital cortex. All injections were within 4–5 deg. of the foveal representation. The injections in area 18 were made on the caudal lip of the lunate sulcus, i.e. adjacent to area 17. Only two or three injections were made in each animal because of the short survival time necessary to prevent diffusion of $^3$H-GABA and its eventual non-specific slow uptake by both neurons and glia. After a postinjection survival time of 20–60 min the animals were perfused with saline, followed by a fixative containing 2.5% glutaraldehyde and 0.5% paraformaldehyde dissolved in 0.1M phosphate buffer, pH 7.2–7.4. Small blocks of the injected cortex were processed for Golgi impregnation and gold toning (Fairén et al. 1977) as described earlier (Somogyi et al. 1981a). Some of the Golgi sections which were initially poorly impregnated were recycled with the section-Golgi impregnation procedure (Freund and Somogyi 1983). The sections were mounted in Durcupan ACM resin on slides and the various impregnated neurons around the injection track were mapped, photographed and drawn with the help of a camera lucida. Thereafter the sections were re-embedded and 1 μm semithin sections were cut through the perikarya of the gold toned neurons for autoradiography. Slides were dipped in Ilford K5 or K2 emulsion, exposed for 3–90 days at 4 °C, developed in Kodak D19B, and fixed. The sections were counterstained with a mixture of toluidine blue and Azur II.

## Results

It has been shown that in autoradiographs of sections embedded in plastic and then gold toned, silver grains are a result of the decay of tritium and not of spurious chemical development of the emulsion (Somogyi et al. 1981b, 1983b; Bolam et al. 1983). In the present material silver grains were clustered over certain neuronal perikarya and diffusely distributed in the neuropil (Fig. 1A). The neuropil labelling gradually decreased with distance from the injection site, and also with longer survival times.

Labelled neurons were present up to 2–2.5 mm from the injection track and their distribution followed a specific laminar pattern depending on which laminae were injected, as described previously (Somogyi et al. 1981a, 1983a). A particularly conspicuous group of small labelled neurons was observed in layers II and upper III following injections of $^3$H-GABA into layers V and VI (Fig. 1A, B). These neurons were directly above the injection track and so far from the site of isotope delivery that the density of silver grains covering their perikarya was strikingly high relative to that above the surrounding neuropil (Fig. 1A–D). On the other hand neurons close to the injection site were surrounded by heavily labelled neuropil (Fig. 1F). Whether such neurons were labelled or not was therefore decided by comparing them with nearby perikarya which had not accumulated GABA and which were always much less densely labelled than the neuropil (Fig. 1F).

In the course of the present study 47 non-pyramidal cells with smooth dendrites, 19 spiny stellate cells and about 150 pyramidal cells, all Golgi-impregnated, were examined for the selective uptake of $^3$H-GABA. The pyramidal neurons were not specially selected; their perikarya happened to be within the same region of the sections as those of non-pyramidal neurons selected for investigation. All the Golgi-impregnated neurons which were examined for uptake of $^3$H-GABA lay within the area around the injection track where labelled perikarya could be seen in the autoradiograms. Furthermore, in order to minimise the possibility of obtaining false-negative results, Golgi-impregnated neurons were

**Fig. 1A.** Light micrograph of a 1 μm thick section through area 18 about 2 mm from the border of area 17 and in the posterior lip of the lunate sulcus. The cortex was injected with $^3$H-GABA at the border between layer VI and the white matter (*asterisk*) and the section was processed for autoradiography. There are labelled neurons (*arrows*) around the injection track and vertically above it up to and within layer II. One neuron (*double arrow*) is shown at higher magnification in **B**. **B**, **D** and **F** are autoradiograms of sections cut at the level of the perikarya of Golgi-impregnated and gold toned neurons (Nos. 1, 2 and 11 in Fig. 3) shown at the same magnification in the previously photographed thick Golgi section in **C**, **E** and **G**, respectively. These gold toned neurons are labelled by $^3$H-GABA as revealed by accumulation of silver grains over the perikarya. *Asterisks* mark neighbouring unlabelled neurons. *Arrows* in B mark $^3$H-GABA labelled neurons which were not Golgi impregnated. Scales: **A**: 100 μm; **B–G**: 10 μm

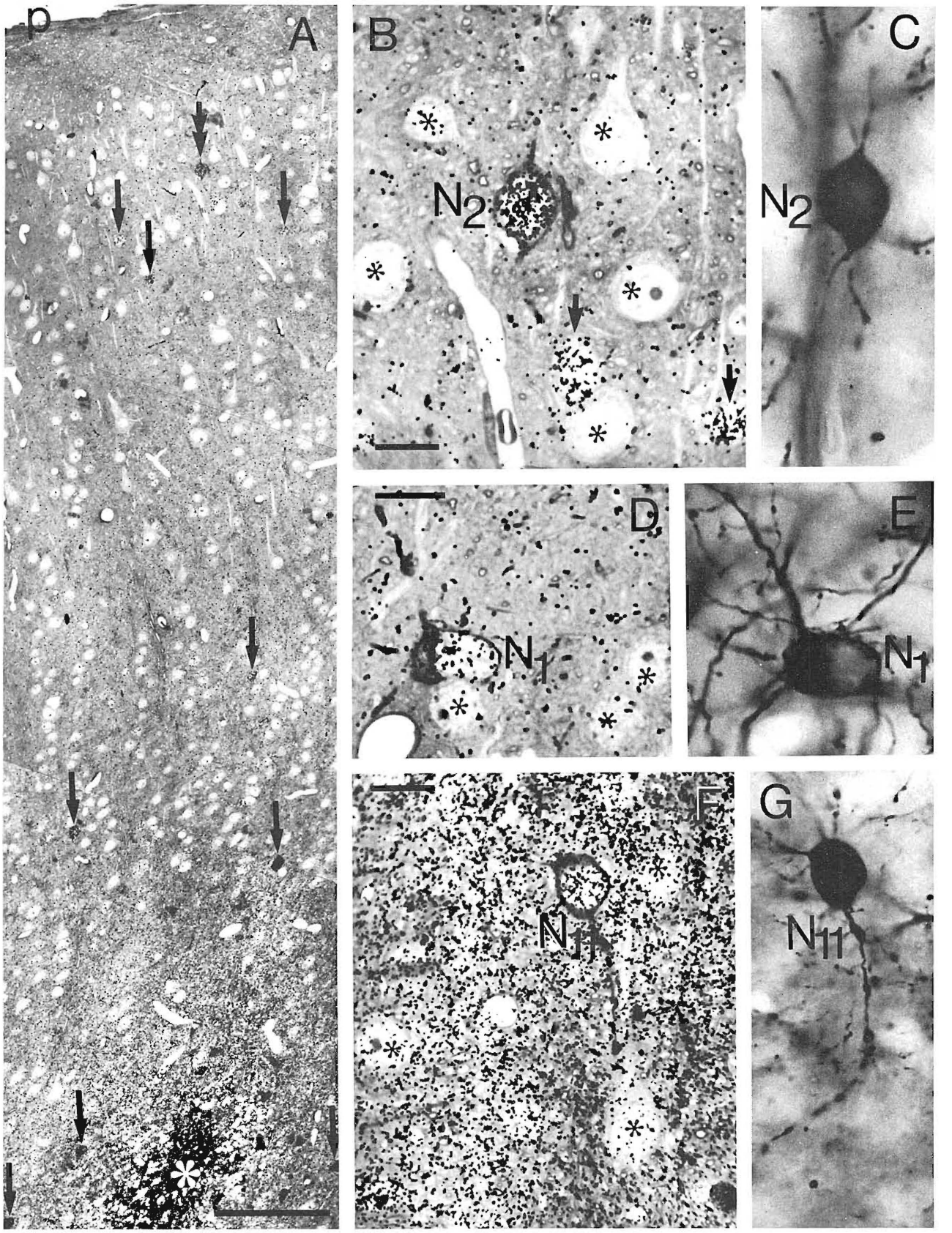
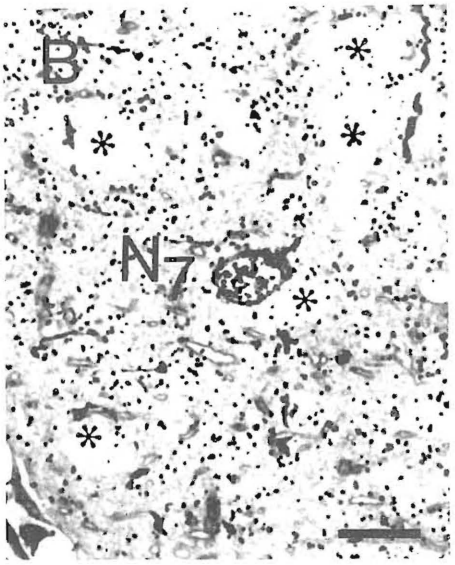
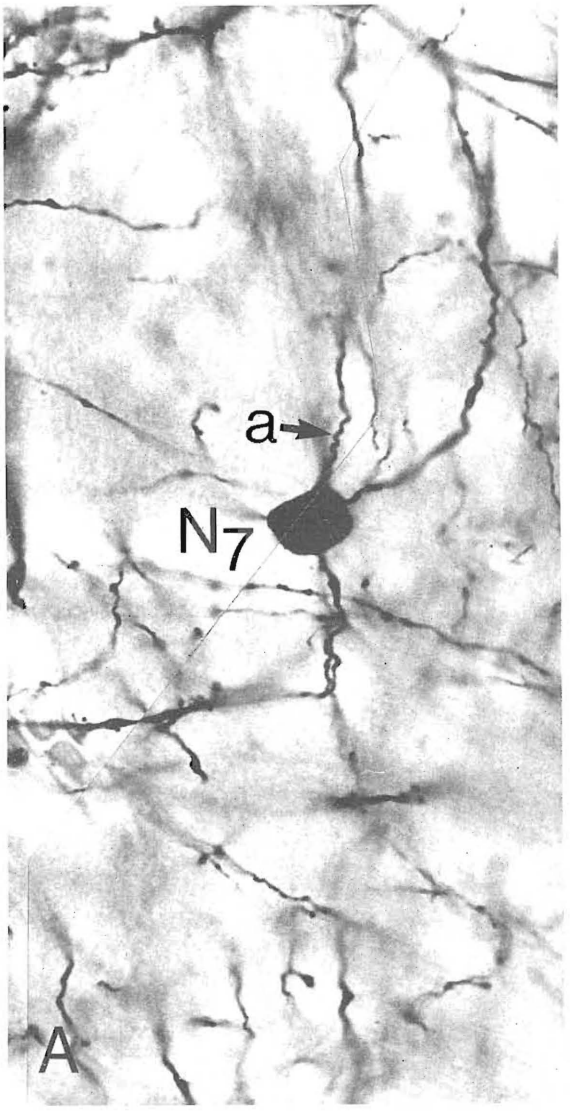



**Fig. 1**



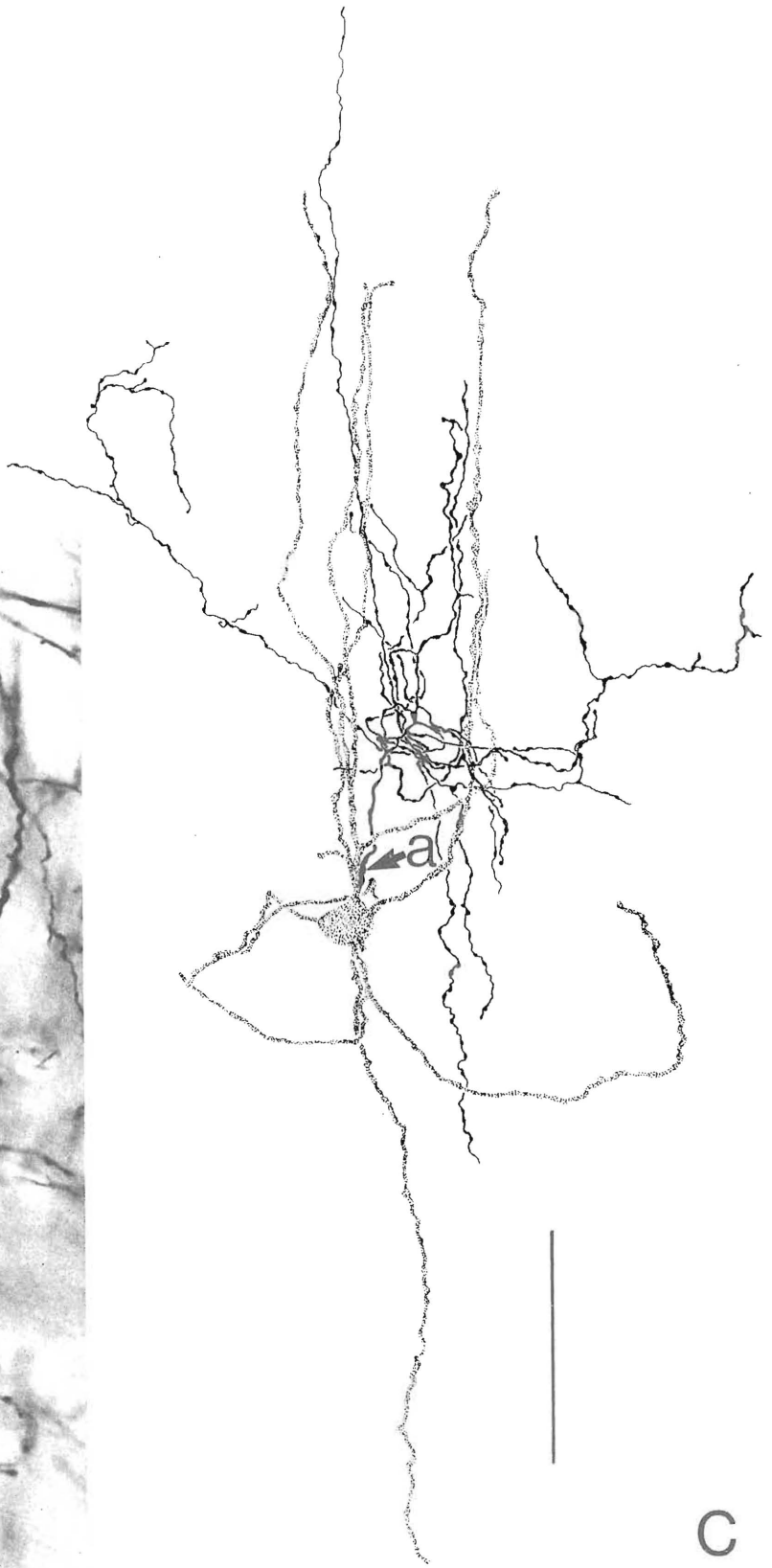




**Fig. 2.** Light micrograph (**A**) and drawing (**C**) of a Golgi-impregnated neuron with local axon (a) in layer III of the monkey's striate cortex. This neuron was labelled by uptake of $^{3}$H-GABA injected into layer III as shown on an autoradiogram of a semithin section (**B**) cut from the perikaryon. *Asterisks* mark unlabelled neurons. Scales: **A**, **B**: 10 μm; **C**: 50 μm

only included in this sample if some labelled perikarya lay even further from the injections track, i.e. neurons at the periphery of the labelled region were excluded. The relatively small sample of non-pyramidal cells reflects the greater difficulty of impregnating this cell-type and the consequent low probability that their processes will be within a region of GABA injection. From this sample 16 aspiny non-pyramidal neurons were labelled. As four of these were examined in 1 μm sections before we started to make prior camera lucida drawings of the thick sections, only 12 neurons are represented in the summary diagram in Fig. 3. Most Golgi-impregnated neurons that were also radiolabelled were found in the upper layers. This does not necessarily mean that neurons which accumulate $^3$H-GABA are more numerous in upper layers. As the surface of the occipital lobe has a variable curvature, and the incident angle of the micropipette was not constant, most injections involved chiefly the upper or the lower cortical laminae. This point is taken up in the Discussion.

Of the 12 neurons accumulating $^3$H-GABA and shown in Fig. 3, eight (Nos. 2–9) are of the bitufted type with their dendrites oriented predominantly radially (Figs. 1A, B; 2 and 3). Most of the smooth, slightly undulating dendrites originate from the upper and lower pole of the soma and are organized into two bouquets. If dendrites leave laterally from their origin, they soon turn radially and join the ascending and descending bouquets. These neurons have medium-size perikarya with diameters of 10–18 μm (Figs. 1A, B and 2A, B).

Neuron No. 10 in Fig. 3 had dendrites whose predominant orientation was apparently horizontal. However, this neuron was incompletely reconstructed because its upper pole was at the surface of the section. The dendrites originating from the cut part of the soma were therefore lost.

Three neurons (Nos. 1, 11 and 12 in Fig. 3) were small aspiny multipolar cells with perikarya measuring 8–10 μm in diameter. Short, frequently branching dendrites originated from all parts of the perikaryon and the dendritic field was round rather than elongated.

Some $^3$H-GABA labelled neurons had perikarya 20–25 μm in diameter. These neurons were observed infrequently in layers III, IVB, V and VI in the autoradiographs, but none of them was Golgi-impregnated.

The axon of only one labelled neuron was impregnated (Fig. 3A, C). The axon initial segment originated from the upper pole of the neuron and branched profusely, giving off varicose collaterals. These collaterals did not form specialized terminal segments like those of the axo-axonic interneuron; neither did they establish pericellular baskets.

## Discussion

Is the labelling of neuronal perikarya by $^3$H-GABA under our conditions a result of an active uptake process and therefore indicative of GABA-ergic neurones? We believe so, because our other autoradiographic studies show that the inclusion in the $^3$H-GABA solution of cis-1, 3-aminocyclohexane carbocylic acid, a competitive inhibitor of neuronal GABA uptake (Bowery et al. 1976) largely prevents perikaryal labelling in the cortex of monkey (Somogyi et al. 1983a) and rat (Somogyi et al. 1983b) and in the neostriatum of the rat (Bolam et al. 1983). Furthermore, neurons which accumulate this labelled amino acid (Hökfelt and Ljungdahl 1972; Chronwall and Wolff 1980; Hendry and Jones 1981; Somogyi et al. 1981a, b; Wolff and Chronwall 1982; Somogyi et al. 1983a, b) are similar in size and distribution to those which contain GAD as revealed by immunocytochemistry (Ribak 1978; Ribak et al. 1979; Hendrickson et al. 1981; Somogyi et al. 1983c) suggesting that $^3$H-GABA reveals neurons which use GABA as their transmitter.

The predominantly supragranular distribution of labelled and impregnated neurons needs comment. Although the injection pipette traversed all layers of the cortex in both area 17 and 18, Fig. 3 indicates only those positions of the pipette which resulted in the labelling of a Golgi-impregnated neuron. In area 17 the supragranular layers were more frequently injected with $^3$H-GABA. Since labelled neurons are usually commonest near the injection site the probability that a Golgi-impregnated cell would also be labelled was much higher in the supragranular than in the infragranular layers in area 17. In addition aspiny non-pyramidal neurons, some of which are the most likely candidates for accumulating $^3$H-GABA, appear more often in the supragranular layers of our Golgi material. These factors may explain why all but one of the neurons in area 17 occurred in the supragranular layers. Their uneven distribution is not strong evidence that they are rare in other layers. In area 18 all three neurons were also in layers II and III, but in this instance they accumulated $^3$H-GABA from a long injection track in layer VI. Here again this does not mean that aspiny neurons which amass $^3$H-GABA selectively are confined to the upper layers. As in area 17, the majority of aspiny non-pyramidal cells that were Golgi-impregnated were found in the supragranular layers.

The present study reveals with the help of Golgi-

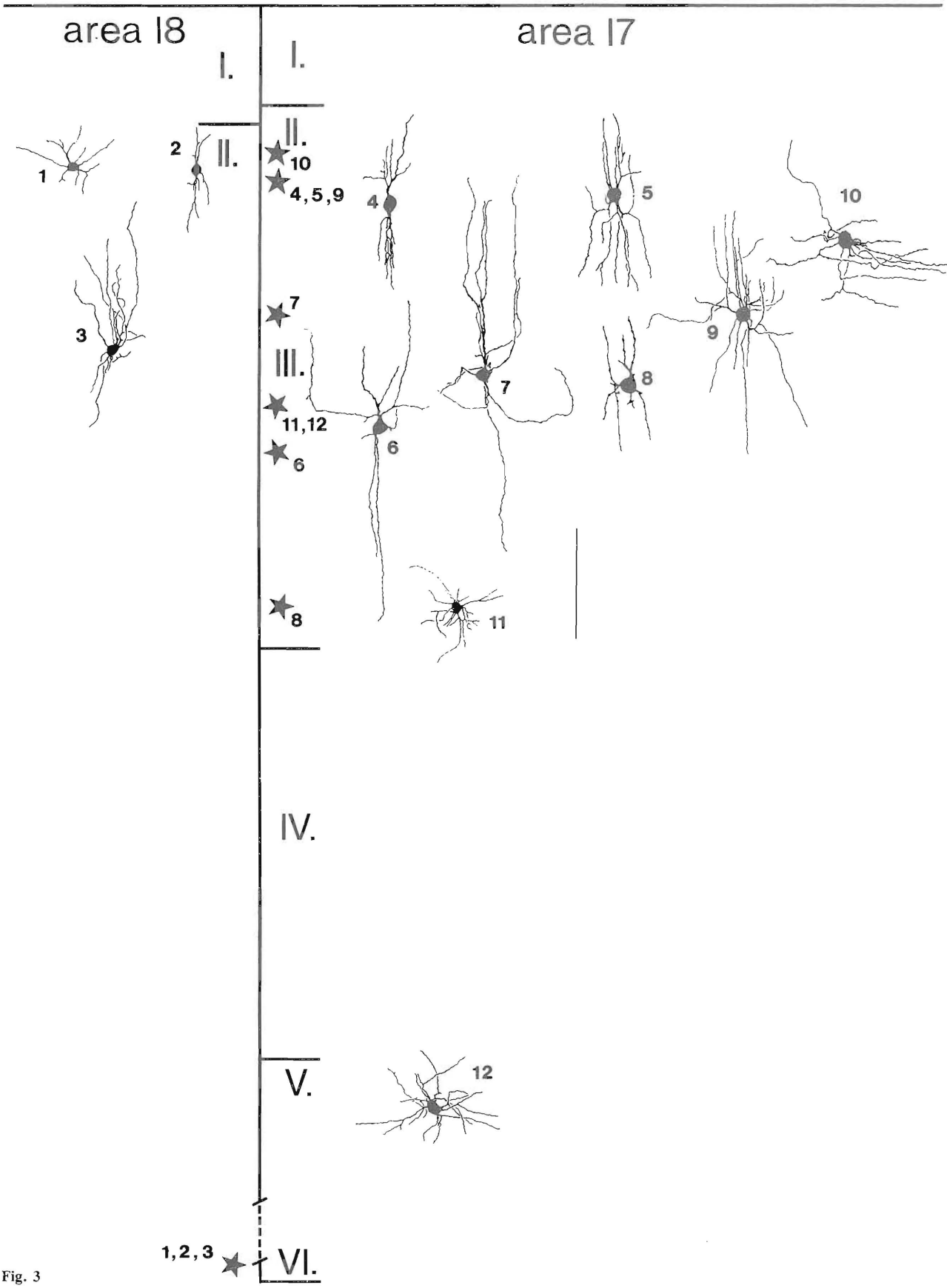

area 18
area 17
I.
II.
III.
IV.
V.
VI.
1
2
3
4
5
6
7
8
9
10
11
12
10
4,5,9
7
11,12
6
8
1,2,3

Fig. 3

impregnation that neurons in the visual cortex of monkeys that accumulate $^3$H-GABA are heterogeneous with regard to their dendritic arborization. This agrees with earlier conclusions based on the size of labelled cell bodies in the somatic-sensory, motor, and parietal areas of monkeys (Hendry and Jones 1981) or on their perikaryal synaptic input in the visual cortex of the rat (Wolff and Chronwall 1982). In the visual cortex of rats Golgi-impregnation of neurons labelled with $^3$H-GABA also showed that they belong to several sub-groups of aspiny or sparsely spiny non-pyramidal cells.

In the monkey we found that the most common type of Golgi-impregnated neuron that also accumulated $^3$H-GABA had a bitufted dendritic arborization of a type frequently encountered in previous morphological studies (Garey 1971; Valverde 1971, 1978; Lund 1973; Lund et al. 1981). Such neurons are sometimes called double bouquet cells but we have argued previously (Somogyi and Cowey 1981) that this term is best used in a narrower sense only for neurons which besides the characteristic dendritic arborization also have a narrow radially oriented axon bundle reaching from layer II to at least layer V (Valverde 1978; Somogyi and Cowey 1981). On the basis of the long descending multibranching axon suggested that these double bouquet cells are labelled by retrograde axonal transport following $^3$H-GABA injections in the deep layers (Somogyi et al. 1981a). The present study provides evidence that in layers II and III of area 18 two of the three neurons which were labelled by retrograde transport of $^3$H-GABA and subsequently Golgi-impregnated had a dendritic arborization characteristic of double bouquet cells. This extends our similar earlier conclusion based on the fine structural characteristics of the neurons labelled by $^3$H-GABA (Somogyi et al. 1981a). Unfortunately, none of the neurons labelled in area 18 had an impregnated axon which, in conjunction with the impregnated dendrites, would unequivocally characterize it. The impregnation of the axon is especially important because another type of cortical interneuron, the axo-axonic or Chandelier cell, which is definitely GABA-ergic (Peters et al. 1982; Freund et al. 1983; Somogyi et al. 1983d), has dendritic features in the monkey (Lund et al. 1981; Somogyi et al. 1982) that are similar to those of double bouquet cells with tight vertical axon bundles (Szentágothai 1971, 1978; Valverde 1978; Somogyi and Cowey 1981). Interestingly some axo-axonic cells in upper layer III have now been shown to have a descending axon to layer VI where it established terminal bouton rows (Lund et al. 1979; Freund et al. 1983). Thus, either axo-axonic cells or double bouquet cells, or both, may be among the $^3$H-GABA labelled neurons in layers III and II after injection of the tracer into the deep layers.

The axon of only one neuron was impregnated, and as far as it could be followed it remained within the dendritic field. This axon did not resemble the axon of axo-axonic cells in the monkey (Lund et al. 1981; Somogyi et al. 1982) or that of the basket cell (Marin-Padilla 1969; Szentágothai 1973; Jones 1975), again indicating that putative GABA-ergic interneurons are of several types within the same small region of cortex.

The small multipolar neurons that accumulate $^3$H-GABA are similar to small aspiny neurons described in previous Golgi studies of the visual cortex of monkeys (Valverde 1971; Lund 1973; Szentágothai 1973). The present study suggests that this type of neuron may also be GABA-ergic. Here again the impregnation of more neurons together with their axons is sorely needed.

Some of the numerous non-impregnated neurons that were labelled with $^3$H-GABA were larger, 20–25 μm, than those which were also Golgi-impregnated. In the monkey's somatosensory cortex similar large labelled neurons have been described (Hendry and Jones 1981). In our Golgi material such large non-pyramidal neurons were rare and as none of them occurred within the area of $^3$H-GABA labelling, we are unable ascertain say whether they accumulate the labelled amino acid. On the basis of their size it was suggested that these large neurons may be basket cells (Hendry and Jones 1981).

In the present study the only impregnated cells which also accumulated $^3$H-GABA were aspiny and non-pyramidal and this is in agreement with the results obtained in another combined Golgi study in the rat (Somogyi et al. 1983b). However, in the monkey as in the rat many Golgi-impregnated neurons within the uptake zone did not accumulate $^3$H-GABA despite having morphological features that are grossly indistinguishable from those of adjacent impregnated and heavily labelled cells. One possibility is that these neurons do not have the apparatus for the selective uptake of $^3$H-GABA and

**Fig. 3.** Drawing of Golgi impregnated neurons which were labelled by selective uptake of $^3$H-GABA in areas 17 and 18 of the monkey's visual cortex. *Stars* mark $^3$H-GABA injection sites in different cortical laminae with numbers denoting neurons labelled from that particular injection. Neuron No. 12 was included from Somogyi et al. 1983a. Neurons Nos. 1, 2, 7 and 11 are shown in light micrographs in Figs. 1 and 2. Scale: 100 μm

that they are probably not GABA-ergic. Another likely explanation is that the axons of such neurons were not within the zone where the concentration of $^3$H-GABA is high enough to yield perikaryal labelling through retrograde transport. Unfortunately this is a limitation of the method and means that even if a Golgi-impregnated neuron is GABA-ergic its labelling by uptake of $^3$H-GABA can be demonstrated only if much of its axon is within the injection zone. Another limitation is that one cannot influence which types of neuron become impregnated by the Golgi procedure in the limited zone where perikaryal labelling occurs. These problems prompted us to use immunocytochemistry to reveal the transmitter candidates of Golgi-impregnated neurons (Freund and Somogyi 1983; Somogyi et al. 1983c; Freund et al. 1983). This procedure gives a higher yield of "double labelled" neurons, but provides no information about the short or long range projection of the neurons. Thus, in studies where the projection areas of neurons, their putative transmitter and the arborization of their processes are collectively of interest, the application of Golgi-impregnation and autoradiography remains a useful combination.

*Acknowledgement.* The authors are grateful to Mrs. Klára Boczkó for her excellent technical assistance.

## References

Bolam JP, Clark DJ, Smith AD, Somogyi P (1983) A type of aspiny neuron in the rat neostriatum accumulates $^3$H-γ-aminobutyric acid: combination of Golgi-staining, autoradiography and electron microscopy. J Comp Neurol 213: 121–134

Bowery NG, Jones GP, Neal MJ (1976) Selective inhibition of neuronal GABA uptake by cis-1, 3-amino-cyclohexane carboxylic acid. Nature 264: 281–284

Chronwall B, Wolf JF (1980) Prenatal and postnatal development of GABA-accumulating cells in the occipital neocortex of rat. J Comp Neurol 190: 187–208

Cowey A, Freund TF, Somogyi P (1981) Organization of $^3$H-GABA-accumulating neurones in the visual cortex of the rat and the rhesus monkey. J Physiol (Lond) 320: 15–16P

Emson PC, Lindvall O (1979) Distribution of putative neurotransmitters in the neocortex. Neuroscience 4: 1–30

Fairén A, Peters A, Saldanha J (1977) A new procedure for examining Golgi-impregnated neurons by light and electron microscopy. J Neurocytol 6: 311–337

Freund TF, Martin KAC, Smith AD, Somogyi P (1983) Glutamate decarboxylase-immunoreactive terminals of Golgi-impregnated axo-axonic cells and of presumed basket cells in synaptic contact with pyramidal cells of the cat's visual cortex. J Comp Neurol (in press)

Freund TF, Somogyi P (1983) The section-Golgi impregnation procedure. I. Description of the method and its combination with histochemistry after intracellular iontophoresis or retrograde transport of horseradish peroxidase. Neuroscience 9: 463–474

Garey LJ (1971) A light and electron microscopic study of the visual cortex of the cat and monkey. Proc R Soc Lond Biol 179: 21–40

Hendrickson AE, Hunt SP, Wu J-Y (1981) Immunocytochemical localisation of glutamic acid decarbocylase in monkey striate cortex. Nature 292: 605–607

Hendry SHC, Jones EG (1981) Sizes and distributions of intrinsic neurons incorporating tritiated GABA in monkey sensory-motor cortex. J Neurosci 1: 390–408

Hökfelt T, Ljungdahl A (1972) Autoradiographic identification of cerebral and cerebellar cortical neurons accumulating labelled gamma-aminobutyric acid ($H^3$-GABA). Exp Brain Res 14: 354–362

Iversen LL, Mitchell JF, Srinivasan V (1971) The release of γ-aminobutyric acid during inhibition in the cat visual cortex. J Physiol (Lond) 212: 519–534

Jones EG (1975) Varieties and distribution of non-pyramidal cells in the somatic sensory cortex of the squirrel monkey. J Comp Neurol 160: 205–268

Krnjevic K, Schwartz S (1967) The action of γ-aminobutyric acid on cortical neurones. Exp Brain Res 3: 320–326

Lund JS (1973) Organization of neurons in the visual cortex, area 17, of the monkey (Macaca mulatta). J Comp Neurol 147: 455–496

Lund JS, Hendrickson AE, Ogren MP, Tobin EA (1981) Anatomical organization of primate visual cortex area VII. J Comp Neurol 202: 19–45

Lund JS, Henry GH, Macqueen CL, Harvey AR (1979) Anatomical organization of the primary visual cortex (area 17) of the cat. A comparison with area 17 of the Macaque monkey. J Comp Neurol 184: 599–618

Marin-Padilla M (1969) Prenatal and early postnatal ontogenesis of the human motor cortex. II. The basket-pyramidal system. Brain Res 14: 633–646

Peters A, Proskauer CC, Ribak CE (1982) Chandelier cells in rat visual cortex. J Comp Neurol 206: 397–416

Ribak CE (1978) Aspinous and sparsely-spinous stellate neurons in the visual cortex of rats contain glutamic acid decarboxylase. J Neurocytol 7: 461–479

Ribak CE, Harris AB, Vaughn JE, Roberts E (1979) Inhibitory, GABAergic nerve terminal decrease at sites of focal epilepsy Science 205: 211–213

Somogyi P, Cowey A (1981) Combined Golgi and electron microscopic study on the synapses formed by double bouquet cells in the visual cortex of the cat and monkey. J Comp Neurol 195: 547–566

Somogyi P, Cowey A, Halász N, Freund TF (1981a) Vertical organization of neurons accumulating $^3$H-GABA in the visual cortex of the rhesus monkey. Nature 294: 761–763

Somogyi P, Cowey A, Kisvárday ZF, Freund TF, Szentágothai J (1983a) Retrograde transport of $^3$H-GABA reveals specific interlaminar connections in the striate cortex of monkey. Proc Natl Acad Sci USA 80: 2385–2389

Somogyi P, Freund TF, Cowey A (1982) The axo-axonic interneuron in the cerebral cortex of the rat, cat and monkey. Neuroscience 7: 2577–2608

Somogyi P, Freund TF, Halász N, Kisvárday ZF (1981b) Selectivity of neuronal [$^3$H]-GABA accumulation in the visual cortex as revealed by Golgi staining of the labelled neurons. Brain Res 225: 431–436

Somogyi P, Freund TF, Kisvárday ZF (1983b) Different types of $^3$H-GABA accumulating neurons in the visual cortex of rat. Characterization by combined autoradiography and Golgi impregnation. Exp Brain Res (in press)

Somogyi P, Freund TF, Wu J-Y, Smith AD (1983c) The section Golgi impregnation procedure. II. Immunocytochemical demonstration of glutamate decarboxylase in Golgi-impregnated neurons and their afferent synaptic boutons in the visual cortex of the cat. Neuroscience 9: 475–490

Somogyi P, Smith AD, Nunzi MG, Gorio A, Takagi H, Wu J-Y (1983d) Glutamate decarboxylase immunoreactivity in the hippocampus of the cat. Distribution of immunoreactive synaptic terminals with special reference to the axon initial segment of pyramidal neurons. J Neurosci (in press)

Szentágothai J (1971) Some geometrical aspects of the neocortical neuropil. Acta Biol Acad Sci Hung 22: 107–124

Szentágothai J (1973) Synaptology of the visual cortex. In: Jung R (ed) Handbook of Sensory Physiology, Central Processing of Visual Information, VII/3B. Springer, Berlin Heidelberg New York, pp 269–324

Szentágothai J (1978) The neuron network of the cerebral cortex: a functional interpretation. Ferrier Lecture. Proc R Soc Lond Biol 201: 219–248

Valverde F (1971) Short axon neuronal subsystems in the visual cortex of the monkey. Int J Neurosci 1: 181–197

Valverde F (1978) The organisation of area 18 in the monkey. A Golgi study. Anat Embryol 154: 305–334

Wolff JR, Chronwall BM (1982) Axosomatic synapses in the visual cortex of adult rat. A comparison between GABA-accumulating and other neurons. J Neurocytol 11: 409–426

Received March 18, 1983