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Neuronal types in the neocortex-dependent lateral territory of the human thalamus

A Golgi-pigment study

Heiko Braak and Eva Braak

Zentrum der Morphologie (Dr. Senckenbergische Anatomie), Theodor Stern Kai 7, D-6000 Frankfurt/Main 70, Bundesrepublik Deutschland

Summary. Nerve cell types of the neocortex-dependent nuclei of the human thalamus were investigated with the use of a transparent Golgi technique, that allows one to study not only the peculiarities of the cell processes, but also the marking characteristics of the intraneuronal lipofuscin pigment deposits. Three principal types of neurons have been distinguished:

Type I is a medium-sized to large neuron with a profusely radiating dendrite system. Numerous large vacuolated lipofuscin granules are cotained in one pole of the cell body.

Type II is a small to medium-sized neuron with a few sparsely branching dendrites. Small and intensely stained pigment granules are dispersed within the cell body.

Type III is a medium-sized to large neuron with only a few thick and almost unbranched dendrites devoid of spiny appendages. The dendrites extend over long distances. The cell body is devoid of lipofuscin granules.

Key words: Thalamus – Golgi technique – De-impregnation technique – Lipofuscin – Projection neuron – Local circuit neuron

Introduction

Numerous attempts have been made to architectonically parcellate the neocortex-dependent territories of the human thalamus (Vogt and Vogt 1941; Hassler 1950, 1959; Dekaban 1953; Andrew and Watkins 1969; Dewulf 1971, van Buren and Borke 1972; Gerebtzoff et al. 1973). In view of their functional significance, surprisingly little is known, so far, about the types of nerve cells forming these portions of the thalamus.

Nissl preparations reveal only somatic features of nerve cells and, therefore, cannot reliably be used for the distinction of projection neurons from local circuit neurons. Golgi preparations, in contrast, display the minute details of the cell processes which are necessary for a classification of a given nerve cell. Only a non-representative small percentage of the nerve cells present in the tissue is depicted by the Golgi techniques. On this account, it is impossible to evaluate the numerical relation of the various cell types to each other in Golgi preparations.

Offprint requests to: Prof. Dr. H. Braak, Zentrum der Morphologie, Theodor Stern Kai 7, 6000 Frankfurt/Main 70, Federal Republic of Germany

The brain of the human adult is rich in intraneuronal lipofuscin pigment. The size, shape, stainability, and pattern of distribution of the pigment are characteristic of each type of nerve cell (Braak 1978, 1980, in press). This can be readily demonstrated by means of a newly developed Golgi de-impregnation technique that allows one to perceive the pigment deposits of individual nerve cells through a transparent impregnation of their somata and processes (E. Braak and H. Braak 1983, H. Braak and E. Braak 1982a, b, 1983, in press). The aim of the present study

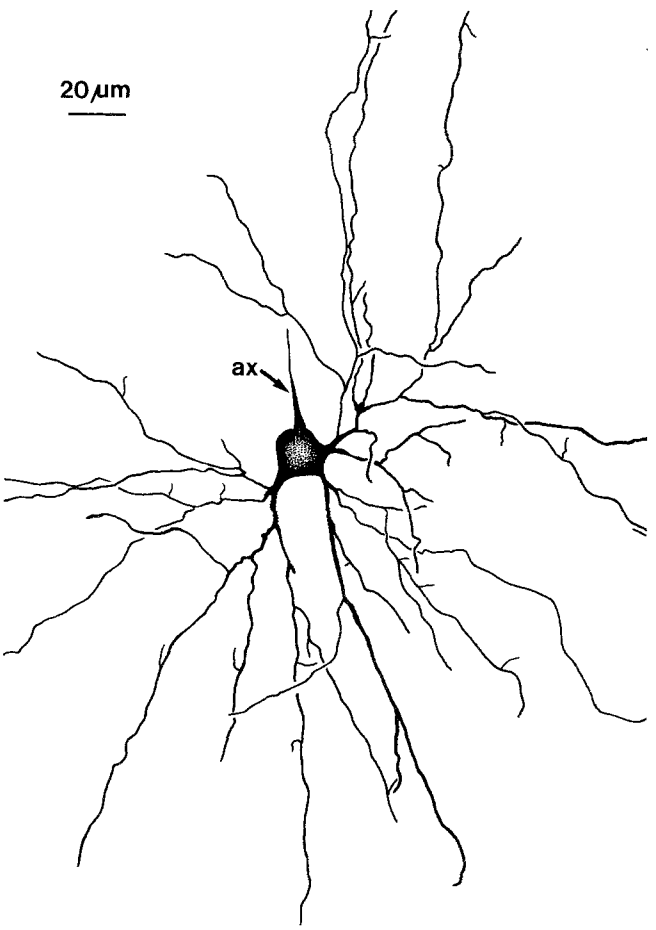


Fig. 1. Camera lucida drawing of a Golgi impregnated type I nerve cell with radiating dendrite system (lateral territory, thalamus, man). Note the thread-like appendages along the dendrites. *ax* axon

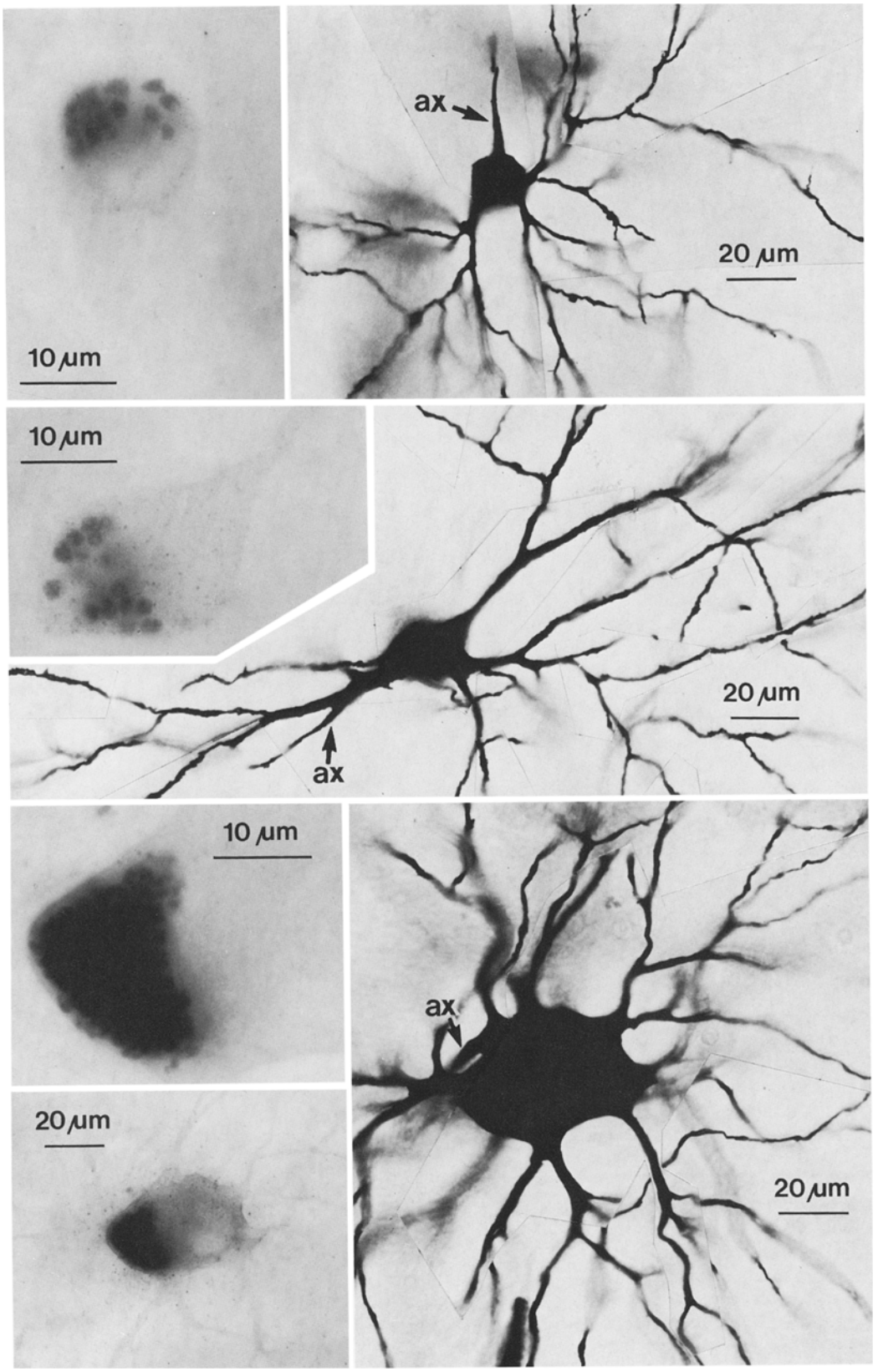


Fig. 2. Photomicrographs of typical type I neurons with numerous dendrites radiating in all directions (lateral territory, thalamus, man). The soma size of these neurons ranges from small to large. (Figure 1 shows the camera lucida drawing of the cell depicted in the upper row.) *ax* axon. Golgi impregnation, 100 µm. *Insets* Same nerve cells, de-impregnated and counterstained for pigment. Type I neurons contain large and irregularly shaped lipofuscin granules which tend to accumulate at one pole of the cell body. Golgi de-impregnation, aldehydefuchsin, 100 µm

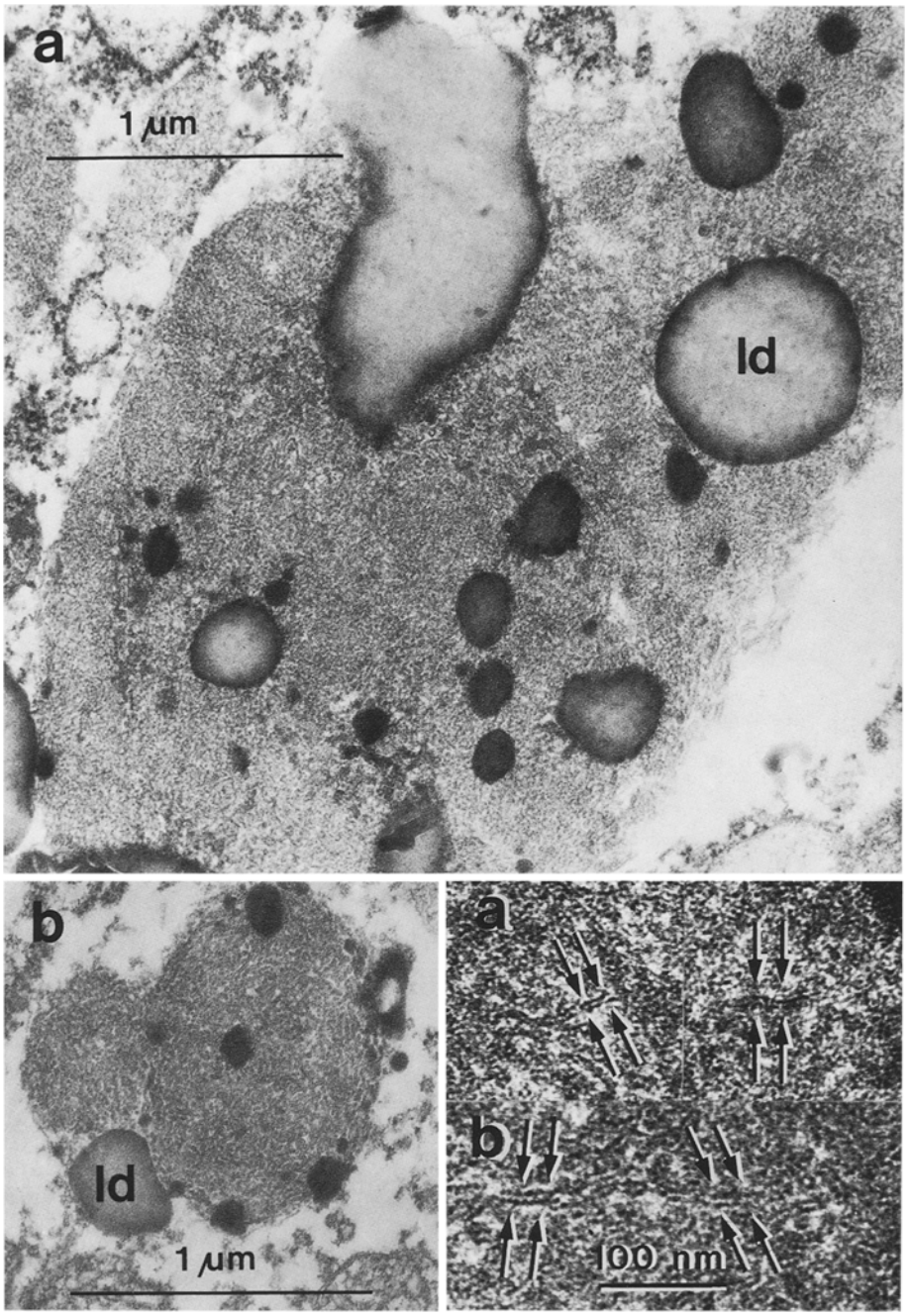


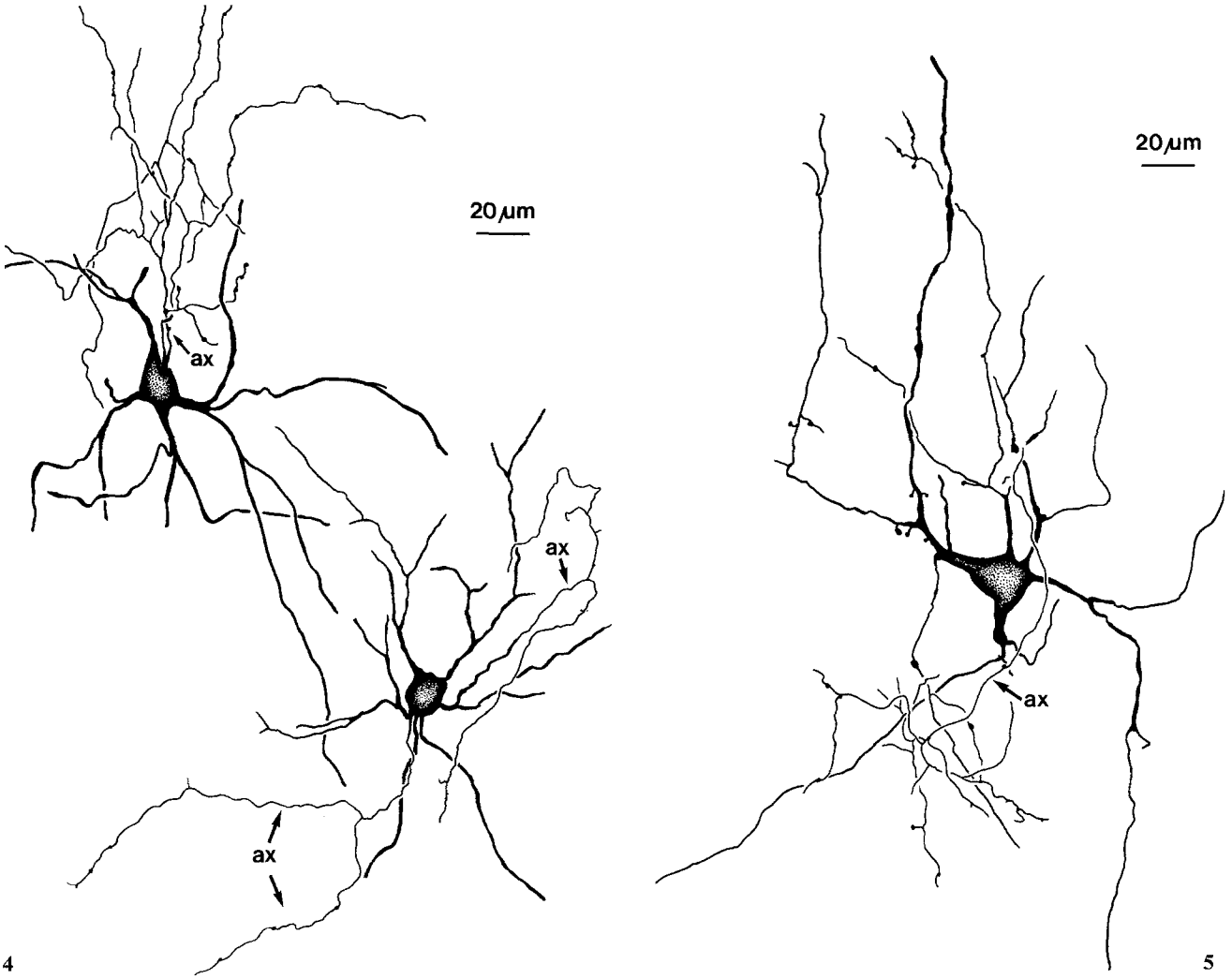
Fig. 3. Electron micrographs of lipofuscin granules within a type I neuron (**a**) and a type II neuron (**b**). The coarse granules of type I neurons and the small ones of type II neurons contain numerous lipid droplets (*ld*) of variable size and electron density embedded within a dense matrix. Lower right corner: The tubular subunits of the dense matrix of type I neuron pigment granules (**a**) are smaller than those of type II neurons (**b**) (*arrows*)

is, therefore, not only to distinguish the various nerve cell types constituting the neocortex-dependent nuclei of the lateral territory within the human thalamus but also to demonstrate their marking pattern of pigmentation.

Material and methods

Seven brains obtained at autopsy and free of significant pathology were used for this study. The brains were fixed by immersion in aqueous solution of formaldehyde (4%). The age range was selected not only to achieve the characteristic pigmentation pattern of nerve cells of the human adult but also to avoid age-related changes of the dendritic arbor (♂ aged 44, cardiac infarction; ♂ aged 45, peritonitis; ♀ aged 48, pneumonia; ♂ aged 51, cardiac infarction; ♂ aged 52, cardiac infarction; ♀ aged 66, carcinoma of the mamma).

Blocks, 3–5 mm thick, including thalamic projection nuclei were cut out of the brains and processed according to the Golgi technique proposed by Braitenberg et al. (1967; see also Millhouse 1981). After impregnation, the blocks were cut at 100 µm with the aid of a freezing microtome. Sections were directly transferred to 70% ethanol, dehydrated and mounted in a synthetic resin (Permount, Fisher). A total of 136 well-impregnated nerve cells were chosen for documentation (84 type I neurons, 45 type II neurons, 7 type III neurons). The vast majority of impregnated neurons belonged to the type I cells. Numerous photographs were taken of each of the documented cells at different magnifications and various depths of focus. In addition,



Figs. 4, 5. Camera lucida drawings of Golgi impregnated type II neurons (lateral territory, thalamus, man). Only a few dendrites are given off from the soma. The axon *ax* branches profusely close to the cell body. Cells of this type may generate more than one axon (lower half of Fig. 4)

camera lucida drawings were made with the aid of a drawing tube. The sections containing the documented neurons were subsequently floated free of the slide and the cover slip by soaking in xylene. Thereafter, the sections were rehydrated and de-impregnated (for details of the de-impregnation technique see Braak, 1983). Sections were then oxidized with performic acid and stained for lipofuscin granules with aldehydefuchsin (Braak 1980). Preparations treated in this way revealed the typical features of both the cell processes and the intracellular accumulations of lipofuscin pigment. Due to the thickness of the sections (100 µm), the clarity within the photographs is reduced to some extent.

Additional blocks of the same material were embedded in paraffin and cut at 12 and 30 µm. Sections were stained with cresylviolet or with a combination of aldehydefuchsin and gallocyanin chromealum, referred to as pigment-Nissl preparations. Thick sections (800 µm) stained with aldehydefuchsin were used for pigmentoarchitectonic studies (Braak 1980, in press).

Small pieces of the lateral nuclear complex of the thalamus were osmicated and embedded in araldite. Sections (2 µm) were stained with methylene blue – azure II to identify the various cell types. The following thin sections were mounted either on mesh grids or on Formvar-coated single hole grids. The thin sections were grid-stained with saturated uranyl acetate in 70% methanol and lead citrate. A Zeiss electronmicroscope 109 (Kodalith MP II ortho), operated at 80 kV, was used (original magnification 3,000 and 20,000).

Results

The neocortex-dependent lateral territory of the thalamus is a heterogeneous gray formed of three principal types of nerve cells which occur in all its subdivisions.

Type I neurons

The most frequently Golgi-impregnated nerve cell type exhibits a polygonal cell body from which numerous dendrites radiate (Fig. 1). These repeatedly break up into smaller twigs. Branching occurs even at distal portions of the dendrites. The main dendrites do not appreciably differ in length and, therefore, a dense and mostly globular dendritic field is generally achieved. The dendrites of cells located

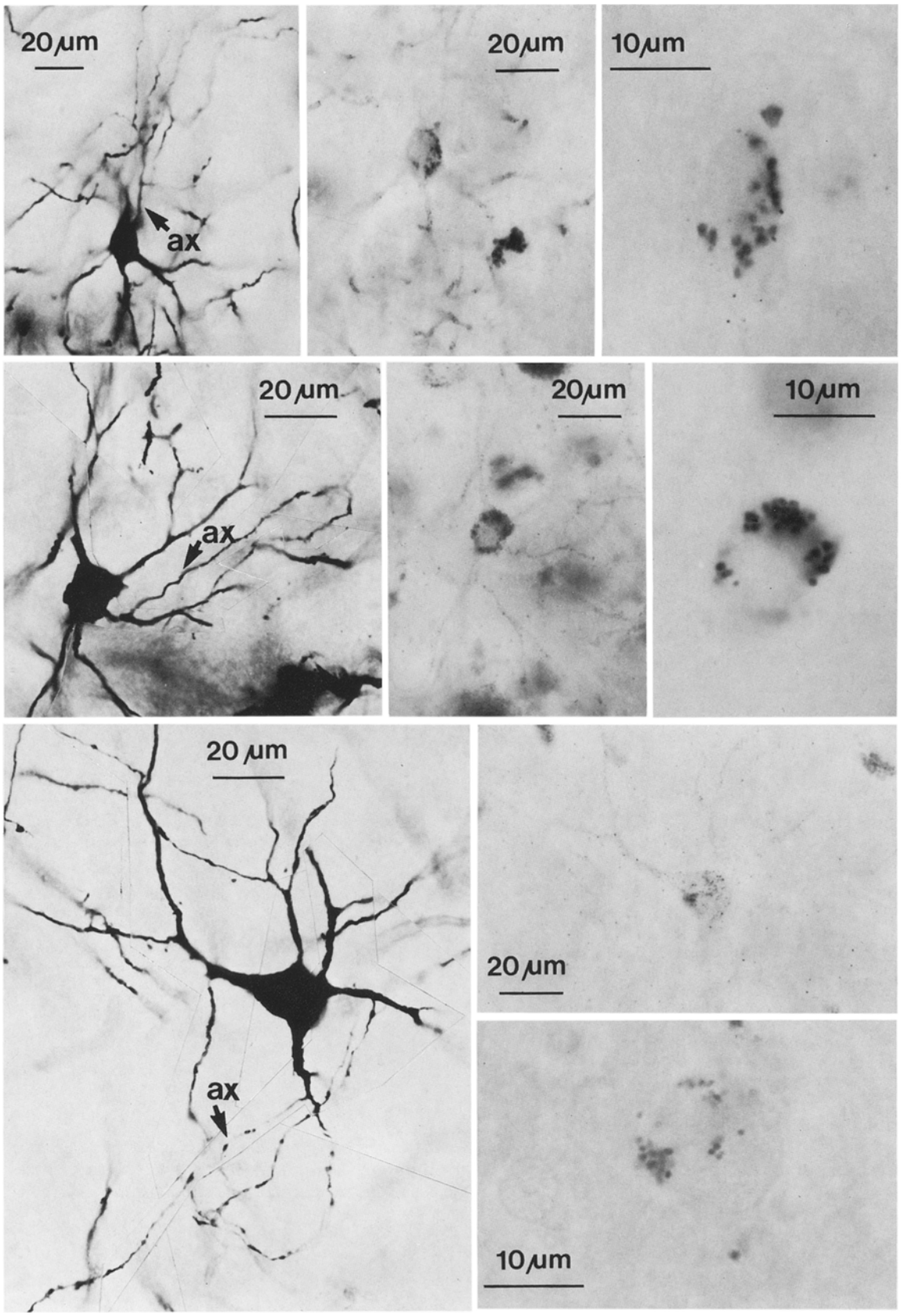


Fig. 6. Photomicrographs of the cells depicted in Fig. 4 (upper half) and Fig. 5 (lower half). *ax* axon. Golgi impregnation, 100 µm. The insets show the same nerve cells after de-impregnation and counterstaining for pigment. Type II neurons contain small and intensely stained lipofuscin granules. Golgi de-impregnation, aldehydefuchsin, 100 µm

along the lateral margin of the lateral thalamic territory do not extend into the adjoining white substance. Such marginal cells may deviate from the above description in that they develop a bush-like dendritic arbor with branches mainly oriented in one direction. The dendrites are devoid of typical spines. Instead, a characteristic feature is the presence of fine thread-like appendages which resemble elongated stalks of normal spines without terminal knob (Figs. 1, 2 upper row).

The axon emerges from the cell body by way of a thick conical process. Normally, its impregnation ceases close to its origin (Figs. 1, 2).

Transparent Golgi impregnations counterstained for lipofuscin pigment reveal that the type I neurons are endowed with numerous large and irregularly shaped pigment granules (up to 5 μm in diameter) which are only weakly stained by aldehydefuchsin. The granules do not lie tightly packed together but tend to accumulate at one pole of the cell body. Numerous unstained lipid droplets can be observed within the granules (Fig. 2).

In the electron microscope some of the lipid droplets (0.1–2.0 μm in diameter) appear particularly dense. They are dispersed within a matrix formed of tubular and bilinear subunits with an outer diameter of about 5 nm and an inner one of about 3 nm (Fig. 3a).

Pigment-Nissl preparations reveal lightly stained multipolar cells with eccentrically located nucleus. A very large nucleolus is contained within the pale nucleoplasm. The inner portion of the nucleus facing the pigment accumulation exhibits numerous infoldings of the nuclear envelope (Fig. 9a–f).

Type II neurons

Type II neurons occur in large numbers and are evenly disseminated throughout all portions of the neocortex-dependent thalamic nuclei. In general, their cell bodies are smaller than those of the type I cells in their vicinity. Frequently, the cell body is elongated and spindle-shaped, but may also show several root-like protrusions extending in different directions. Only a few dendrites are generated from the soma. These bifurcate sparsely close to their origin to form a relatively large ellipsoidal dendritic domain with a low density of branches (Figs. 4–6).

The axon originates either from the soma or from the proximal portion of a dendrite and begins to arborize profusely in the immediate vicinity of the parent soma. The terminal branches are very fine processes with knob-like thickenings irregularly spaced apart. The axon cannot be traced far beyond the limits of the dendritic domain. Occasionally, cells of this type generate more than one axon. As to its calibre and branching pattern, the additional axon closely resembles the main axon (Fig. 4).

Transparent Golgi impregnations counterstained for pigment show that – without exception – type II cells are endowed with small lipofuscin granules (0.5–1.0 μm in diameter) widely disseminated throughout the cell body (Fig. 6). These granules have a considerably greater affinity for aldehydefuchsin than the large granules of the type I cells. Intermediate forms do not occur. Therefore, type II cells stand out in pigment preparations despite the small diameter of their lipofuscin granules.

Electron micrographs show that the granules are composed of a few small lipid droplets (up to 0.5 μm in diameter) and an electron dense matrix. Often only one light lipid droplet is contained in the matrix which consists of tubular subunits; these are slightly larger (outer diameter about 7 nm, inner diameter about 4 nm) than those found in the pigment of type I neurons (Fig. 3b).

Pigment-Nissl preparations display irregularly shaped cell bodies, well supplied with basophilic material. The eccentrically located nucleus is generally dark with fine clumps of chromatin evenly dispersed within the nucleoplasm (Fig. 9g–i, l–n). Some medium-sized type II cells occasionally exhibit a more lightly stained nucleus (Fig. 9k, o).

Type III neurons

The third neuronal constituent of the neocortex-dependent thalamic nuclei is rarely encountered in Golgi preparations. Cells of this type, nevertheless, occur in all portions of the nuclei but fairly wide apart.

The soma size varies from medium-sized to large. The polygonal cell body generates only a few but thick and extended dendrites that spread out in all directions. The diameter of the dendrites remains fairly constant for quite an extent. If at all, the dendrites undergo initial ramification

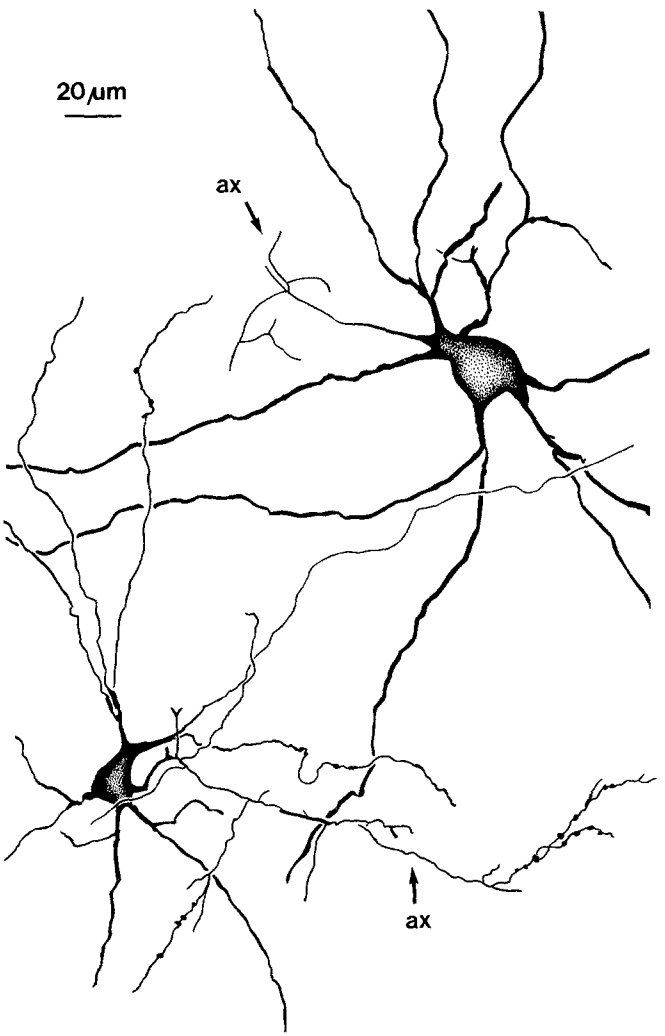


Fig. 7. Camera lucida drawings of Golgi impregnated type III neurons (lateral territory, thalamus, man). The medium-sized to large cell body generates a few extended dendrites. The axon *ax* splits up close to the parent soma

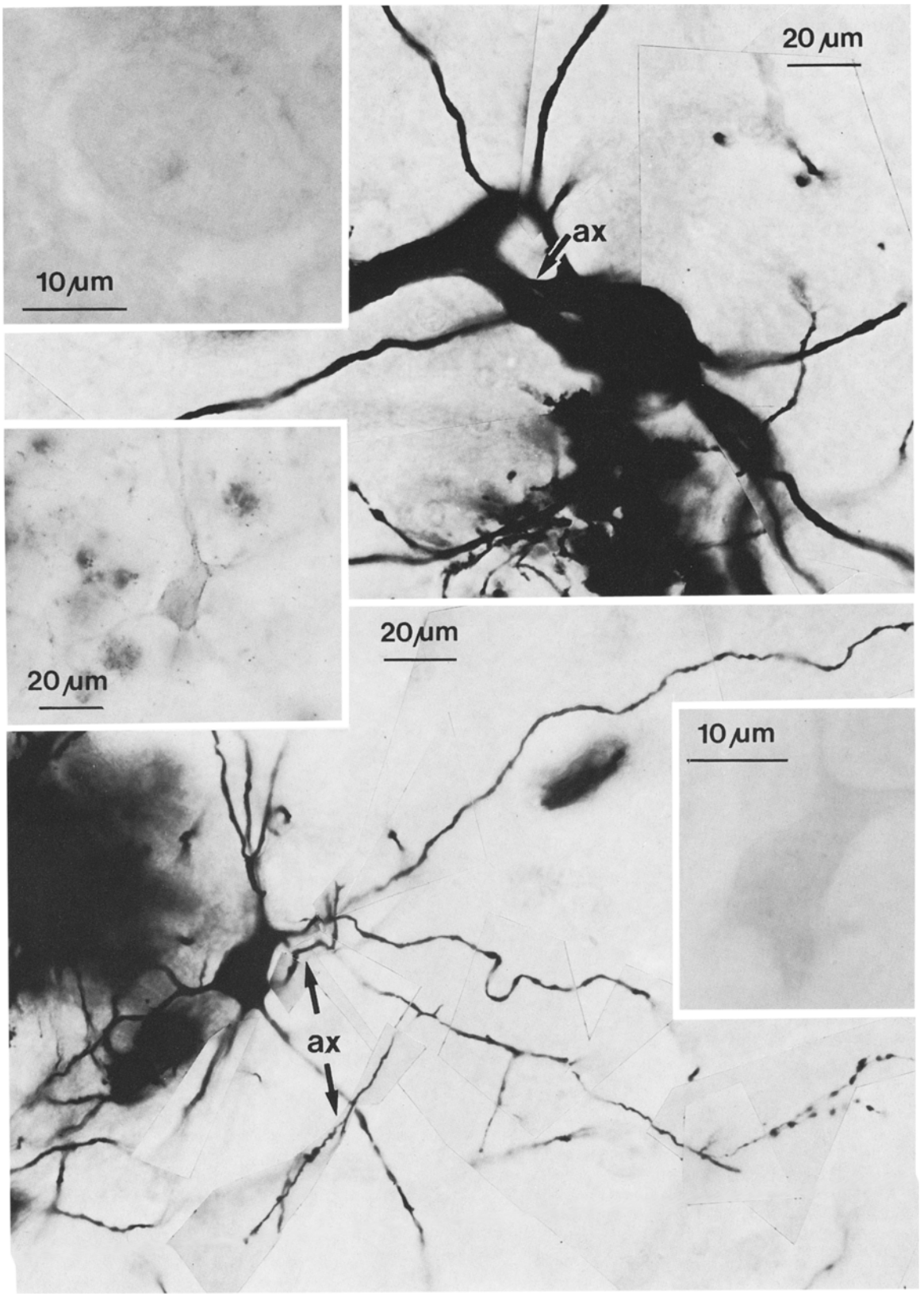
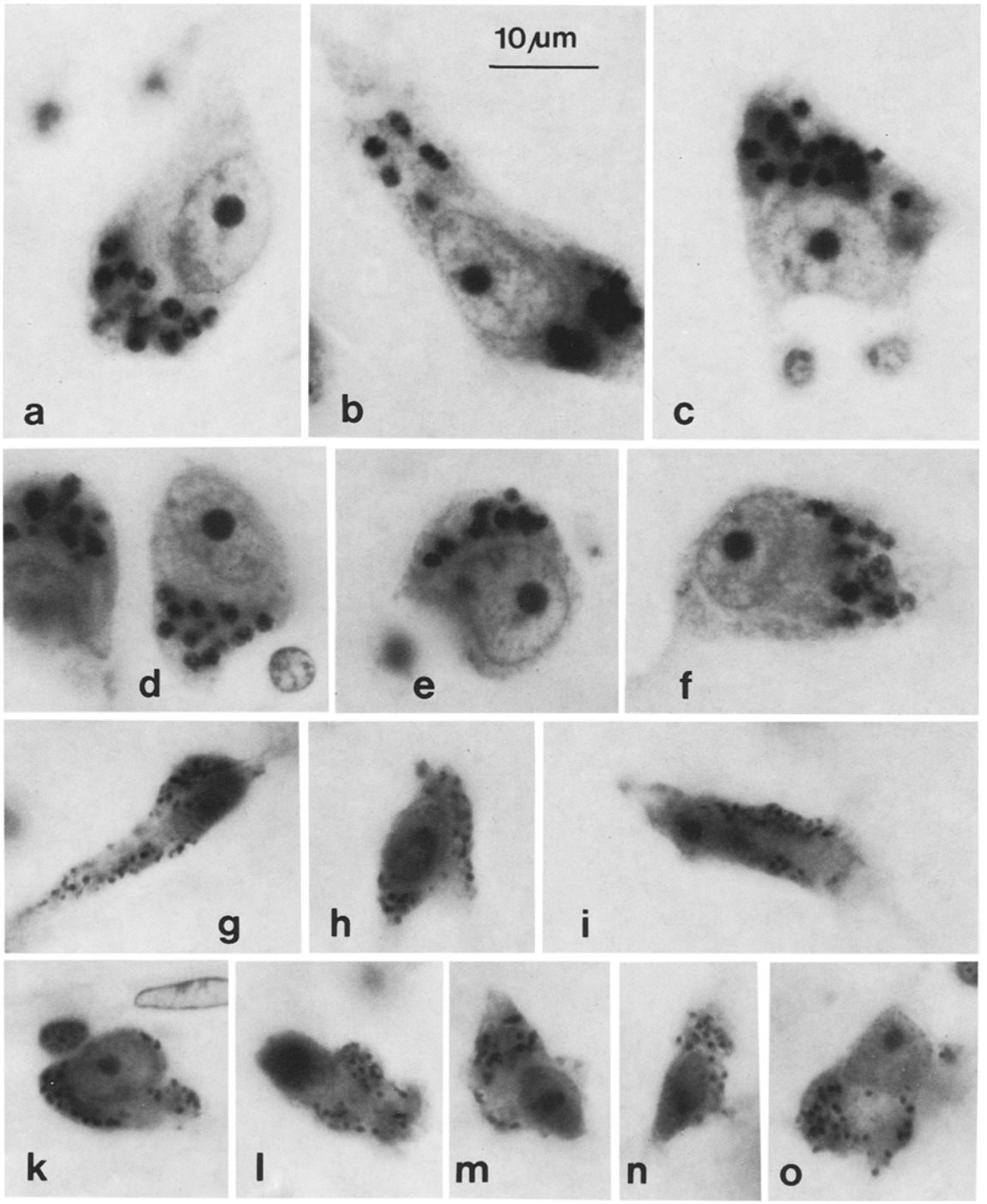


Fig. 8. Photomicrographs of the cells shown in the camera lucida drawings of Fig. 7. The insets display the same nerve cells after de-impregnation and counterstaining for pigment. Type III neurons are devoid of lipofuscin granules. Golgi impregnation and de-impregnation, aldehydefuchsin, 100 µm



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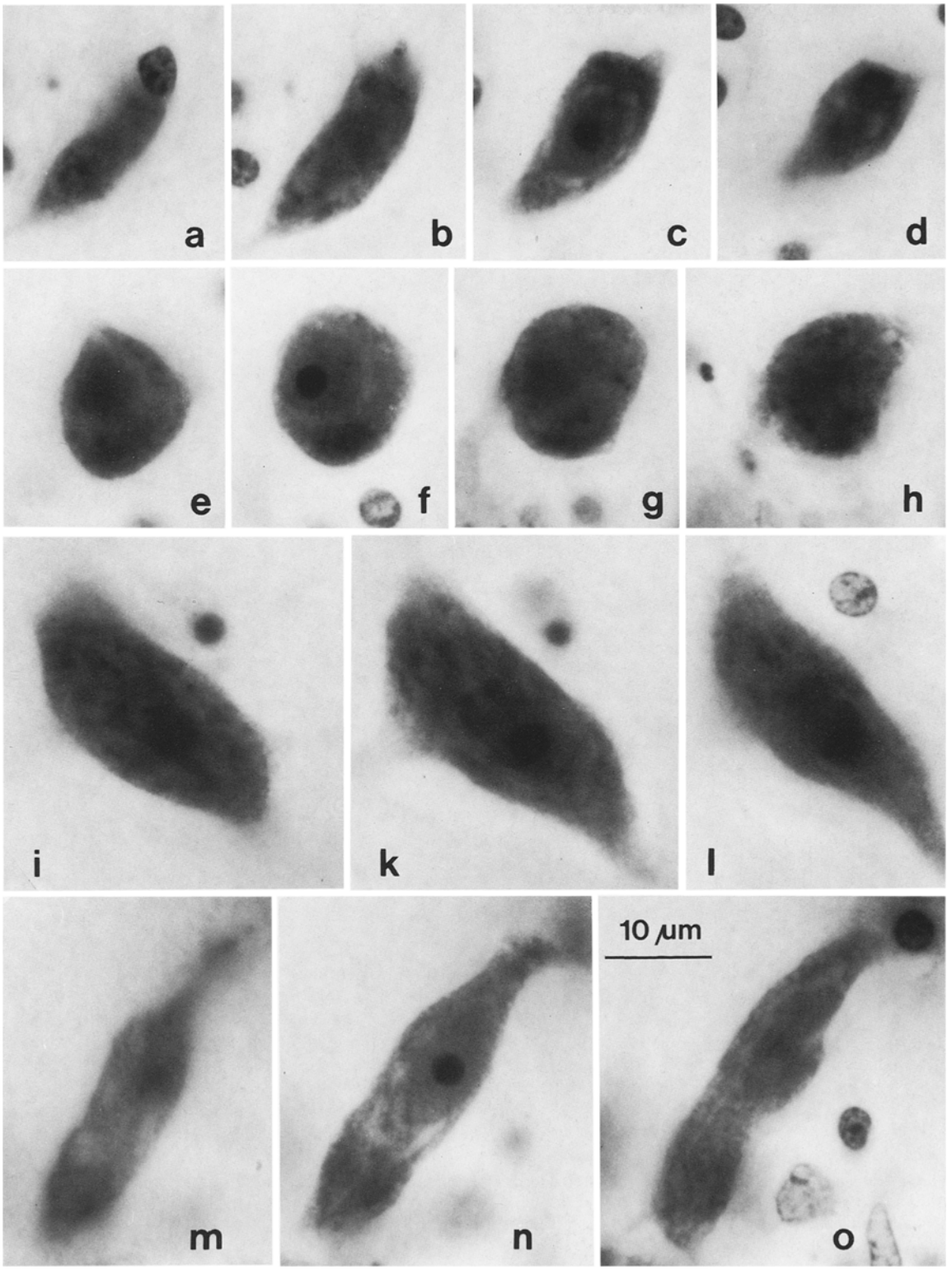
Figs. 9, 10. Nerve cells of the neocortex-dependent thalamus (lateral territory, man) as seen in the combined pigment-Nissl preparation. **Fig. 9a–f** Type I neurons with coarse pigment. The individual granules contain numerous light lipid droplets. The pale nucleus is usually in an eccentric position. **Fig. 9g–o** Type II neurons with irregularly shaped cell body and eccentrically located dark nucleus. Cells of this type contain small, intensely stained lipofuscin granules. Intermediate forms do not occur. Type I neurons and type II neurons are easily distinguished on account of their characteristic pigmentation. **Fig. 10** Type III neurons with dark nuclei and well-developed clumps of basophilic material within the cytoplasm. Four cells are depicted, each at different depths of focus (**a–d, e–h, i–l, m–o**) to demonstrate that cells of this type are devoid of pigment. Performic acid aldehydefuchsin – gallocyanin chromealum, 30 µm

close to the parent soma. They are devoid of spines or other appendages and adopt a straight course. The dendritic domain is extended but there is only a low density of dendritic branches within its boundaries (Figs. 7, 8).

The axon originates either directly from the cell body or from a dendrite. It splits up close to the parent soma. Unfortunately, the impregnation of the axon is often incomplete. Some of the impregnated axons, nevertheless, show fine terminal twigs with irregularly spaced globular thickenings. The terminal branches do not extend far beyond the limits of the dendritic domain (Figs. 7, 8).

Transparent Golgi impregnations counterstained with



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aldehydefuchsin reveal that cells of this type are devoid of lipofuscin pigment (Fig. 8). In pigment-Nissl preparations, these cells exhibit an ellipsoidal or globular nucleus. A single large nucleolus and a huge amount of evenly dispersed chromatin is contained within the nucleoplasm. The cell body is richly endowed with basophilic material and often irregularly formed large Nissl bodies can be recognized (Fig. 10).

Dwarf neurons

Indications for the existence of axonless dwarf cells with a soma size of less than 6 µm can neither be found in our Golgi material, nor in pigment-Nissl preparations. Cells of this type have been noted to occur in the thalamus of the adult cat (Scheibel et al. 1972).

Ectopic neurons

Occasionally, some medium-sized and multipolar nerve cells can be encountered which are immediately conspicuous due to the presence of a fair number of typical spines along their dendrites. On this account, cells of this type are easily distinguished from the normal constituents of the neocortex-dependent thalamic nuclei. Spiny neurons occur regularly within the cortex-independent territories of the thalamus and, therefore, we consider these elements as ectopic nerve cells. Now and then, cells of this type lie tightly packed together forming small islands not far away from intralaminar nuclei to which they possibly belong.

Discussion

Golgi pigment analysis reveals that the neocortex-dependent nuclei of the lateral thalamic territory comprise three principal cell types. The most frequently occurring cells are the type I projection neurons. Numerous type II local circuit neurons are scattered throughout the nuclei whereas the non-pigmented type III cells can only rarely be encountered (Fig. 11).

Type I neurons

Type I neurons of the human thalamus with a radiating dendrite system referred to as "bush-cells" have been described and illustrated by Kölliker (1896). A comparable neuronal type has been found in thalamic nuclei of several subhuman mammalian species as well (Ramon y Cajal 1911, mouse, rabbit, cat; Scheibel and Scheibel 1966a, b, mouse, rat, cat; Tömböl 1966/67, cat; Ralston and Herman 1969, cat; Mathers 1972, squirrel monkey; Somogyi et al. 1973, cat; Hajdu et al. 1974, cat; Dekker and Kuypers 1976, rat; Ogren and Hendrickson 1979, macaca monkeys; Madarasz et al. 1983, cat).

Transparent Golgi impregnations counterstained with aldehydefuchsin offer the advantage of allowing direct observation of the pigmentation pattern of nerve cells identified by characteristic features of their cellular processes. The type I neurons have a common pattern of pigmentation in all subdivisions of the thalamus. Although cells of this type may greatly differ in the size of their cell bodies and the elaboration and orientation of their dendritic arbors, their common pattern of pigmentation restrains us from proposing further subdivisions.

Type II neurons

Suitably impregnated type II neurons with local axon are rarely encountered in Golgi preparations. Kölliker (1896) emphasized that cells of this type did not occur in his Golgi material. In the subhuman mammalian thalamus, in contrast, Ramon y Cajal (1911) found small short-axoned cells, the existence of which has been confirmed by Tömböl (1966/67, 1969) in the cat's brain (see also: Ralston and Herman 1969, cat; Mathers 1972, squirrel monkey; Somogyi et al. 1973; cat; Hajdu et al. 1974, cat; Ogren and Hendrickson 1979, macaca monkey; Madarasz et al. 1981, 1983, cat). These authors emphasize that type II neurons appear particularly well-impregnated with the Kopsch perfusion technique. In the cat, the local circuit neurons are marked by conspicuous filiform appendages along their dendrites, a feature that permits their easy distinction from

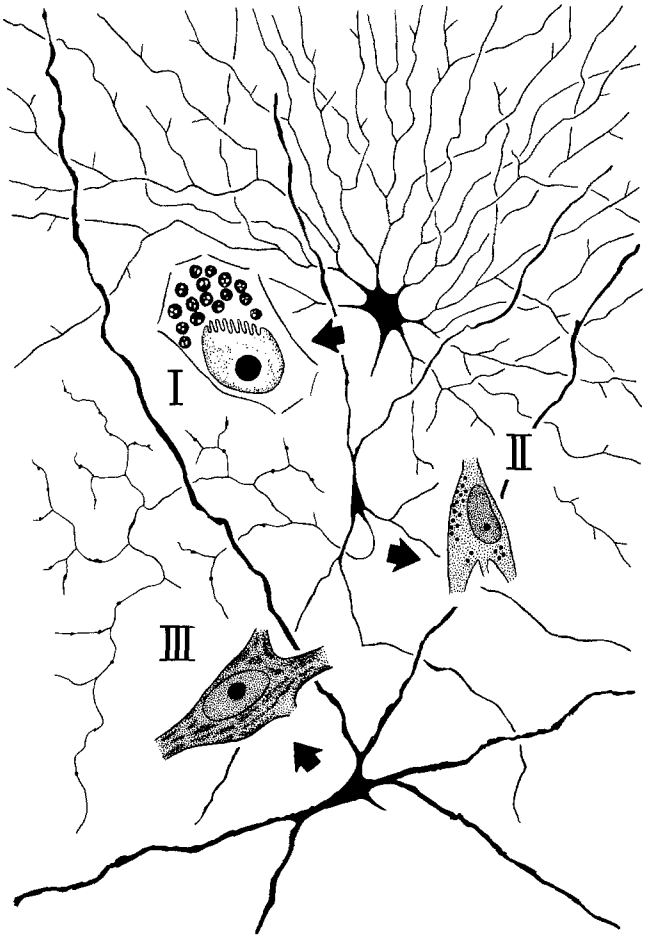

Fig. 11. Summary diagram of the neuronal types in the thalamus (lateral territory, human adult). Type I neurons are easily distinguished from type II and type III neurons in Golgi impregnations. Transparent Golgi preparations counterstained for pigment reveal that each of these cell types shows a characteristic pattern of pigmentation. The three neuronal types can, therefore, reliably be recognized in pigment Nissl preparations as well

type I neurons (Tömböl 1966/67, Rinvik and Grofova 1974). Unfortunately, these processes are rarely impregnated in preparations processed with the classical Golgi techniques, and this might account for the fact that, in our material, we have rarely observed such appendages.

Type II neurons most probably correspond to the thalamic microneurones (McLardy 1950, 1963; Lemieux 1954; Waddy and McLardy 1956; Dewulf 1971) or thalamic internuncial cells (Hassler 1955, 1959, 1964; Namba 1958) recognized in Nissl preparations. Hassler emphasizes that cortical areas receive, besides specific afferents, a second set of smaller fibres from their corresponding thalamic nuclei, suggesting that these originate from internuncial cells (Fig. 3 in Hassler 1959). We have never seen type II neurons with axons extending far beyond the limits of the dendritic domain. Moreover, in experimental animals, cells of this type have not been demonstrated to be filled retrogradely by labeling substances injected into structures outside the thalamus (Keefer et al. 1980). We therefore consider the type II cells to be local circuit neurons.

Transparent Golgi impregnations counterstained for pigment reveal that throughout all subdivisions of the human thalamus, type II neurons are marked by fine, intensely

stained lipofuscin granules which can easily be distinguished from the coarse pigment found in type I neurons. Intermediate forms do not exist. Normally, the type II neurons are smaller than type I cells, although there is considerably overlap between both types. In Nissl preparations, therefore, both types cannot be distinguished from each other with sufficient certainty if quantitative evaluations are attempted. Golgi preparations, in contrast, permit easy recognition of type II cells, but they display only a small and non-representative percentage of the neurons present in the tissue. Type I neurons are far more easily impregnated than type II cells. The combined pigment-Nissl preparation shows all of the nerve cells and since the thalamic neuronal types are very differently pigmented this simple technique not only allows one to reliably classify the nerve cell types but also to evaluate the ratio of projection neurons versus type II and type III neurons. Histochemical, electron microscopic, and neuropathological studies may take advantage of the characteristic pigmentation which reliably indicates the cell type, rendering staining of the cellular processes unnecessary.

Type III neurons

Until now, type III neurons devoid of pigment have not been recognized as normal constituents of the human thalamus. Only a few cells of this type showed a probably incomplete impregnation of their axonal arborization so that we can only tentatively classify these cells as local circuit neurons. In several features, type III neurons are reminiscent of large non-pigmented cortical stellate cells (Braak 1980, in press). In addition, lack of pigmentation has been found in several types of local circuit neurons, not only in the telencephalic cortex but also in subcortical nuclei (H. Braak and E. Braak 1982a, in press).

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