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Author(s): J. R. Wilson, M. J. Friedlander and S. M. Sherman

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Fine structural morphology of identified X- and Y-cells in the cat's lateral geniculate nucleus

BY J. R. WILSON†, M. J. FRIEDLANDER‡, AND S. M. SHERMAN
Department of Neurobiology and Behavior, State University of New York, Stony Brook, New York 11794, *U.S.A.*

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[Plates 1–10]

Four physiologically identified neurons in the A laminae of the cat's dorsal lateral geniculate nucleus were filled with horseradish peroxidase and studied using the electron microscope. Two were X-cells and two were Y-cells. Each had electrophysiological properties appropriate for its X- or Y-cell class, and each also had an axon that projected into the optic radiation, indicative of a geniculocortical relay cell. Representative samples from about 10 % of each neuron's entire dendritic arbor (proximal and distal) were taken to obtain an estimate of the types and distributions of synapses contacting these arbors. One X-cell had a cytoplasmic laminar body, but there were no other significant cytological differences seen among the neurons. Common to each of the neurons were the following synaptic features: (i) retinal terminals (r.l.p.) were mostly or entirely restricted to proximal dendrites or dendritic appendages (< 100 μm from the soma). These terminals constituted about 15–25 % of the synapses on the proximal dendrites. (ii) Terminals with flattened or pleomorphic synaptic vesicles (f. terminals) were predominant on the proximal dendrites (30–55 % of the total synapses for that region) and were mainly located near the retinal terminals. A smaller percentage (10–20 %) were also distributed onto the distal dendrites. (iii) Small terminals with round synaptic vesicles (r.s.d.), many presumably having a cortical origin, predominated (60–80 %) on distal dendrites (> 100 μm), but also formed a large proportion (40–70 %) of the synapses on the intermediate (50–150 μm) dendrites. Total synaptic contacts for one X-cell and one Y-cell were estimated at about 4000 and 5000, respectively.

The major fine structural differences observed between X- and Y-cells were almost entirely related to the retinal afferents. First, the retinal synapses for X-cells were mostly made on to dendritic appendages (spines, etc.), whereas Y-cells had most of their retinal synapses onto the shafts of primary and proximal secondary dendrites (that is, near branch points). Second, the retinal terminals that contacted X-cell dendrites nearly always formed triadic arrangements that included nearby

† Present address, correspondence and reprint requests to: Yerkes Regional Primate Research Center, Emory University, Atlanta, Ga. 30322, U.S.A.

‡ Present address: Department of Physiology and Biophysics, University of Alabama, Birmingham, Al. 35294, U.S.A.

f. terminals, but those on Y-cells rarely did so. Finally, the main type of f. terminals associated with X-cells were morphologically different from most of those associated with the Y-cells, and this also related directly to the triadic arrangements; that is, f. terminals in the triadic arrangements were morphologically distinguishable from f. terminals that did not participate in triadic arrangements. Even though the present sample is quite small, these morphological differences between X- and Y-cells indicate that they might be the synaptic basis for some of the differential processing of information occurring for the two cell types in the lateral geniculate nucleus.

Introduction

The morphological properties of the neurons in the cat's dorsal lateral geniculate nucleus have been extensively studied. At the electron microscopic level, considerable attention has been focused on synaptic morphology, and several different types of synaptic terminals have been identified. However, owing to the difficulty of following processes through long series of thin sections, the overall synaptic patterns have been derived from examining small parts of neurons whose other parts and characteristics are unknown. Thus, many fine structural profiles have yet to be traced to their parent neurons, and the total synaptic inputs that converge onto a single cell have not been described. Furthermore, correlations of electrophysiological properties with morphological types or afferent synaptic inputs have not been technically feasible. With the use of intracellularly injected horseradish peroxidase (HRP), it is now possible not only to characterize the morphology of entire individual neurons, but also to correlate these findings with the electrophysiological characteristics of the neuron.

An important reason for carrying out these studies in the lateral geniculate nucleus is the large body of background research available on this nucleus. This allows the data to be placed into a framework that can be more readily interpreted. Neurons within the A laminae of the lateral geniculate nucleus have been classified electrophysiologically as X-cells or Y-cells. W-cells are present in several areas of the lateral geniculate nucleus (Wilson *et al.* 1976; Dreher & Sefton 1979; Spear *et al.* 1977; Stanford *et al.* 1981, 1983; Sur & Sherman 1982), but they were not examined in this study. The X- and Y-cell classes have been the object of most studies (for recent reviews see Rodieck 1979; Stone *et al.* 1979; Sherman 1979; Lennie 1980; Sherman & Spear 1982). X-cells differ from Y-cells in several electrophysiological properties including axonal conduction velocity, receptive field size, linearity of spatial and temporal summation to visual stimuli, and responses to fast-moving stimuli (Enroth-Cugell & Robson 1966; Cleland *et al.* 1971; Hoffmann *et al.* 1972; So & Shapley 1979; Lehmkuhle *et al.* 1980). Owing to these and many other differences, it is thought that X- and Y-cells mediate different visual functions through separate, parallel pathways.

At the light microscopic level, there are also several morphological types of neurons within the lateral geniculate nucleus. Guillery (1966) divided the neurons of the A laminae into three classes on the basis of differences in soma size and dendritic morphology (for example, the presence of dendritic appendages, their

location on the dendrites, and dendritic arborization patterns). It was originally thought that two of these morphological types (class 1 and 2) might correspond to the electrophysiologically identified Y- and X-cells, respectively, and the third (class 3) to interneurons (for example, Wilson *et al.* 1976; LeVay & Ferster 1977). Subsequently, Friedlander *et al.* (1981) studied the relation of electrophysiological and morphological classes of neurons directly by injecting HRP into physiologically identified neurons. Their study demonstrated that X-cells have smaller somata and thinner dendrites than do Y-cells. X-cell dendrites are oriented along projection lines (Sanderson 1971), typically have many appendages, and are confined to the lamina containing the soma. Y-cell dendrites occupy a spherical arbor, have a few simple appendages, and some dendrites from nearly every Y-cell cross laminar borders. The above properties are consistent with class 1 cells being Y-cells, but the class 2 category contains both X- and Y-cells. All class 3 cells studied were X-cells. These studies using intracellular HRP injections have thus led to a description of the light microscopic structure of physiologically identified neurons.

Because the reaction product of 3-3′-diaminobenzidine and HRP is electron dense, the method of intracellular injection of HRP permits clear fine structural identification of the processes of a single injected neuron. Therefore, in this preliminary study, we have used this technique to examine the fine structure and synaptic inputs of several X- and Y-cells in the A laminae of the lateral geniculate nucleus.

Methods

Electrophysiological procedures

The techniques used for the intracellular injection of HRP in this study are nearly identical to those that have previously been reported from this laboratory (Friedlander *et al.* 1981; Stanford *et al.* 1981; Sur & Sherman 1982). Five adult cats were used. They were anaesthetized with halothane during the initial stages of the preparation. These stages included: venous cannulation for infusion of the paralytic (gallamine triethiodide); a tracheal cannulation for artificial respiration; craniotomies for placement of stimulating electrodes (in the optic chiasm and visual cortex) and for recording or injecting micropipette (in the lateral geniculate nucleus); and contact lenses to protect and focus the eyes onto the tangent screen. As part of our routine surgical procedures, Deltacaine was injected into the external auditory meatuses and around muscle wound margins, and the cats were maintained for recording on a 70:30 mixture of N_2O:O_2. Heart rate, body temperature, and expired CO_2 were continuously monitored.

Glass micropipettes were used to record extra- and intracellular activity. They were filled with a 4% solution (by mass) of HRP (Sigma type VI) in 0.05 M Tris buffer plus 0.2 M KCl (pH 7.6), and they were bevelled to an impedance of 70–120 MΩ measured at 100 Hz. Action potentials of individual neurons of the lateral geniculate nucleus were first isolated extracellularly, and electrophysiological properties of each neuron were characterized to permit their identification as an X- or Y-cell. These properties included latency to optic chiasm stimulation, centre–surround sign (on or off), centre response to standing contrast (tonic or phasic), response to a large, rapidly moving disc appropriate to stimulate the

receptive field surround, receptive field centre size, and the linear or nonlinear response to a counterphase modulated grating pattern (see table 1).

After these properties were determined, the cell was impaled, typically by passing short depolarizing current pulses through the electrode (< 2 nA). A rapid d.c. potential drop of 20–50 mV coupled with the appearance of slow wave synaptic activity indicated that the electrode tip had entered the cell. Most of the cell's properties were rechecked to be certain we had penetrated the same cell that we had studied extracellularly. We then used positive current pulses (2–10 nA at 1–10 Hz) to iontophorese HRP into the cell.

TABLE 1. NEURONAL CHARACTERISTICS

	X1	X2	Y1	Y2
1. optic chiasm latency/ms	2.4	1.8	1.1	1.2
2. linear or nonlinear	linear	linear	nonlinear	nonlinear
3. centre–surround response	on–off	off–on	on–off	on–off
4. centre size/deg	0.5	1.1	1.5	0.8
5. response to fast-moving target	no	no	yes	yes
6. sustained (5 s) or transient (5 s)	sustained	sustained	transient	transient
7. latency to cortical stimulation	—	—	0.7 antidrom	1.1 orthodrom
8. receptive field eccentricity/deg	26	22	4	9
9. laminal location	A	A1	A1	A
10. soma area/μm^2	282	275	760	449
11. Scholl ring analysis†				
total dendritic intersections	68	63	142	74
vertical/horizontal ratio	7.5	20.0	0.92	0.51

† Concentric rings centred on the soma were drawn at 50 μm intervals; dendritic intersections with these rings were then counted. The rings were divided into two horizontal and two vertical quadrants by two lines oriented 45 deg to the 'vertical' line (that is, the vertical line is perpendicular to the laminar borders) and passing through the centre of the circles. The dendritic intersections were then localized with respect to these horizontal or vertical quadrants.

Cell recovery, processing and sectioning

At least one hour after the last cell of the preparation had been injected, the cat was deeply anaesthetized with sodium pentobarbital and transcardially perfused with a solution of 1 % paraformaldehyde, 2 % glutaraldehyde, and 5 % dextrose (all solutions by mass). The perfusate was buffered by 0.15 M phosphate, and a few drops of 0.01 M $CaCl_2$ were added. The brain was removed blocked down to an area containing the lateral geniculate nucleus, stored in additional perfusion solution for another 2–4 h, and transferred to a 0.15 M phosphate buffer-5 % dextrose solution overnight. The tissue was then sectioned at 50 μm on a Vibratome and reacted with 3,3′-diaminobenzidine (DAB) plus H_2O_2. All sections containing the lateral geniculate nucleus were wet-mounted and examined under the light microscope for HRP-injected neurons. Selected sections containing these neurons were then osmicated (2 % (by mass) OsO_4 for 1 h) and dehydrated through a graded alcohol series followed by propylene oxide and Epon embedding. Each piece of tissue was embedded between two pieces of thin plastic so that the injected

cells and their processes could be easily observed with the light microscope and drawn with a drawing tube attachment. Figure 1*a*, *b*, plate 1, shows cell X1 (an X-cell) as it appeared after being embedded. Although osmication darkens the tissue, the DAB–HRP reaction product is still clearly visible for most of the neuronal processes under the light microscope. However, some of the smaller structures such as spine stalks were not easily seen at this stage of processing because the combined plastic coverslip and Epon thickness precluded good optics. All of these smaller structures were visible after the section was cut down to a small square (< 1 mm^2), removed from between the plastic sheets, and mounted on an Epon cutting block. Usually, several 1 μm sections were taken from the top to smooth the surface. We then made use of a 100 × dry metallurgical objective for a detailed inspection and to draw the HRP-filled structures at 1000 × magnification. Finally, the block was thin-sectioned, and these sections (approximately 80 nm thickness) were picked up on Formvar-coated, slotted grids. Figure 1*c* shows a 1 μm thick section of cell X1 taken from the block. The block face was frequently re-examined to relate adjacent thin sections to the tracing of the soma and dendrites.

Results

Electrophysiological properties

Most of our data are based on detailed analyses of four projection neurons that were obtained from four different cats. One other neuron from a fifth cat was briefly examined for specific characteristics that will be pointed out in the text. Table 1 summarizes the electrophysiological characteristics of the more thoroughly examined four neurons, and their fine structural analysis is described below. All four neurons were located in the A laminae of the lateral geniculate nucleus. Two were X-cells (X1 and X2) and two were Y-cells (Y1 and Y2) as determined by electrophysiological criteria (Enroth-Cugell & Robson 1966; Cleland *et al.* 1971; Hoffman *et al.* 1972; Hochstein & Shapley 1976*a*, *b*). Since each neuron had an axon that could be followed into the optic radiation above the perigeniculate nucleus, we presume that they all projected to the cortex; one neuron (Y1) was also antidromically activated by cortical stimulating electrodes. Neuron Y2 was trans-synaptically, rather than antidromically, stimulated by these electrodes, despite its identification as a relay cell (see also Friedlander *et al.* 1981). Experiments from which cells X1 and X2 derived did not incorporate cortical stimulating electrodes.

Light microscopic observations

Drawings of each of the four neurons are shown in figure 2, with the insets illustrating their relative position and dendritic orientation within the nucleus. The morphology of each neuron at the light microscopic level was also characteristic for its neuronal class (X- or Y-cell) using criteria previously described by Friedlander *et al.* (1981). For example, each X-cell had a medium-sized soma, many spines and complex appendages along its dendrites, including 'grape-like clusters' at several primary dendritic branch points. Nearly all of the dendritic appendages had bulbous heads and narrow necks (for example, figure 11). Rarely, a short, stubby

dendritic appendage was observed on a distal dendrite (for example, figure 7*b*). The X-cell dendritic arborizations were largely oriented in a cylinder perpendicular to the plane of the laminae, and none of these dendrites crossed laminar borders. In contrast, the Y-cells had large somata, few dendritic appendages, and no grape-clusters at branch points. Whereas Y1 had radially spreading dendrites in all directions, Y2 had mostly ventrally radiating dendrites in a hemispherical arrangement, perhaps because of its location at the dorsal edge of lamina A. X1 and Y1 have been previously illustrated at the light microscopic level (X1 is neuron 3 and Y1 is neuron 12 in Table 2 of Friedlander *et al.* 1981).

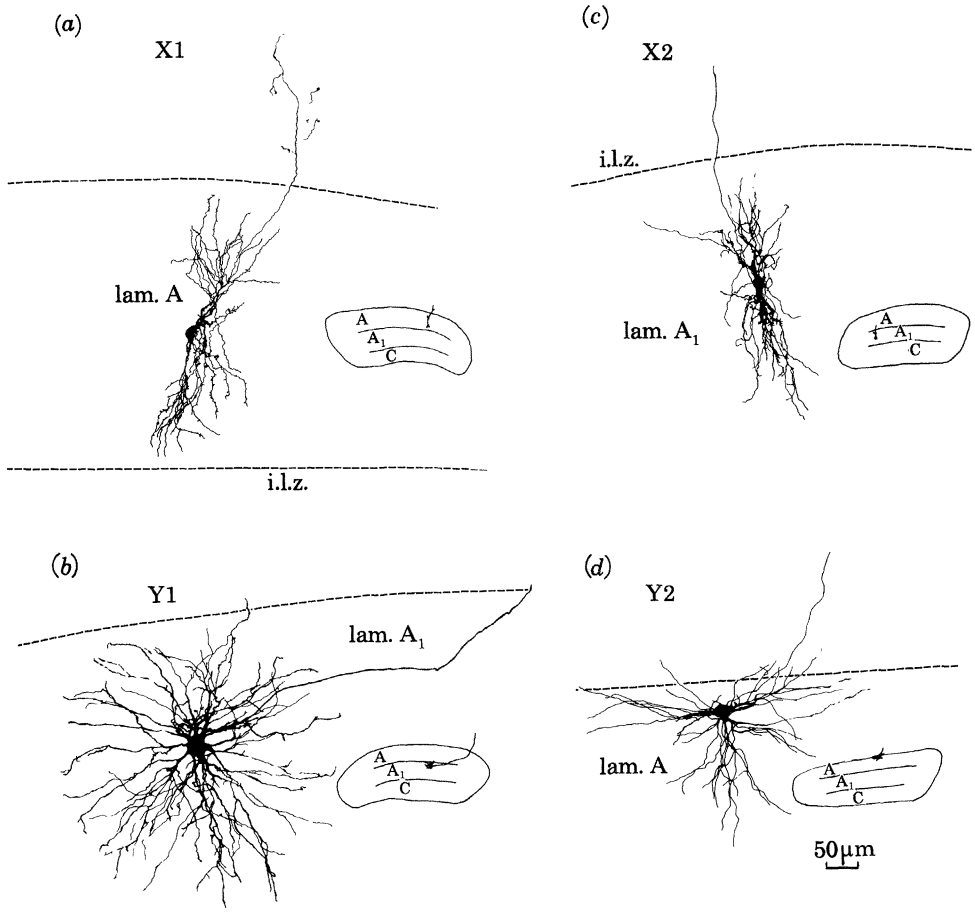

FIGURE 2. Drawings of four geniculate neurons that were filled with HRP and examined with the electron microscope. Figures (*a*) and (*c*) show the X-cells (X1, X2) and (*b*) and (*d*) show the Y-cells (Y1, Y2). Insets indicate the position of each cell within the lateral geniculate nucleus, i.l.z., interlaminar zone.

Electron microscopic observations

Sections for analysis

From the Epon-embedded, 50 μm thick sections of each neuron, one section was selected for serial sectioning and fine structural analysis. The selected section contained part or all of the soma and many proximal and distal dendrites such

that a representative sample of the neuron's dendritic arborization could be analysed. For one X-cell (X1), a second section was also selected because the more peripheral dendrites were not available in the first section. Figure 3 shows line drawings of the parts of the HRP-filled neurons that were included in the 50 μm thick sections used for analysis. By redrawing a neuron after every 48 thin sections (approximately 3.8 μm), we were able to determine accurately what parts of the

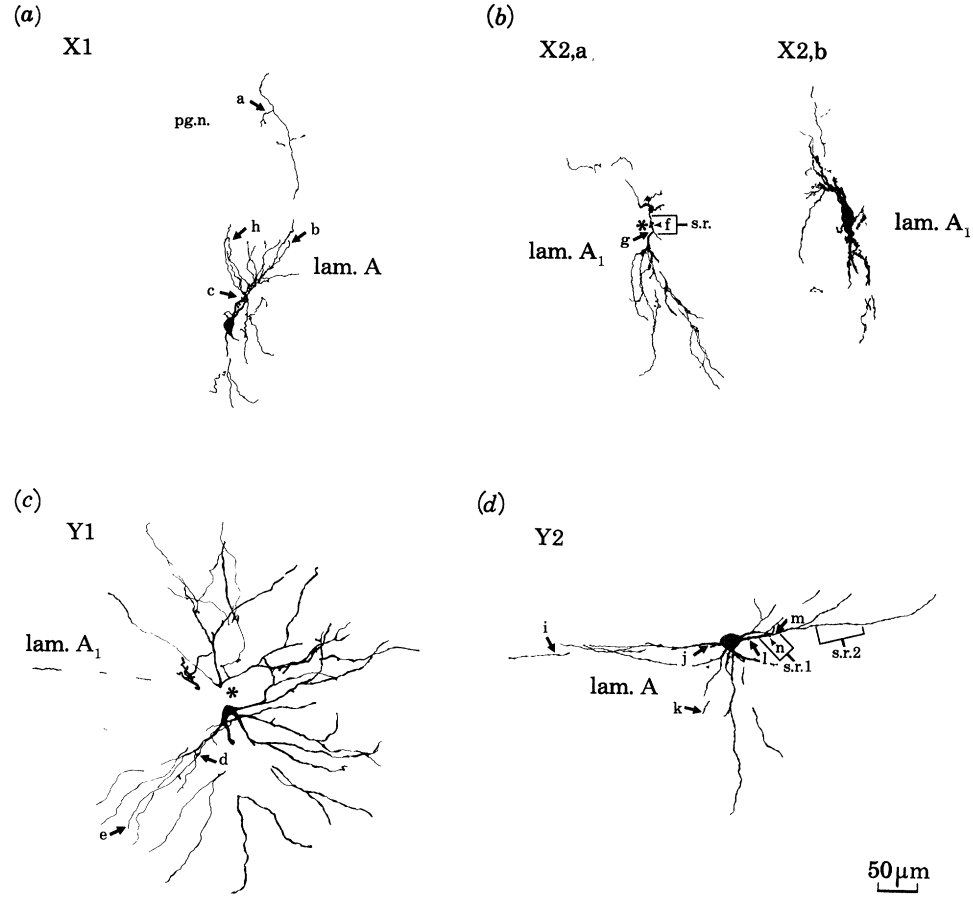

FIGURE 3. Drawings of parts of the neurons shown in figure 2. Each of these drawings represents the part of the neuron included in one 50 μm thick, Epon embedded section that was subsequently examined with the electron microscope. The letters close to the dendrites indicate where electron photomicrographs were taken for the following figures (shown in parentheses in each of the legends). The bracketed areas, labelled s.r., were serially reconstructed for quantitative purposes (see text). Each asterisk in (*b*) and (*c*) indicates the position of the soma relative to the dendrites.

HRP-filled neuron were being examined in each thin section. When present, the location of the soma relative to capillaries and unstained neurons was also helpful in this respect. Thus, the position of synapses onto the dendrites was relatively easy to determine, and the percentage of each synaptic type (r.l.p., r.s.d. or f.; see below) was calculated for various distances along the dendrites.

Terminal, as used in this study, can be considered as a profile containing synaptic vesicles and making at least one synapse. A terminal was considered to have a synapse if there were plasma membrane thickenings on both sides and clustering of synaptic vesicles at the density on one side. Owing to the HRP densely filling the dendrite in some cases, the postsynaptic thickening was not always observed, and we then relied only on the pre-synaptic thickening and clustered vesicles to assume a synapse was present. Each membrane position that displayed these characteristics was counted as a synapse as long as they were separated by non-synaptic membrane. Thus, a terminal profile could have more than one synapse made onto the HRP-filled dendrite, and some terminals did make two synapses within a single section. Synapses cut parallel to the membrane would not have been counted.

Qualitative observations

Examination under the electron microscope was first made on unstained thin sections. The DAB–HRP reaction product caused the profiles containing it to stand out clearly from the surrounding material, and this made it relatively easy to locate all of the sectioned pieces of the neuron before examining them in the adjacent, stained sections. Within these profiles, the reaction product spread diffusely through the intracellular space as seen in figures 4–12, plates 2–10. However, it did not penetrate membrane-bound structures such as mitochondria or synaptic vesicles. Therefore, much of the internal neuronal structure of the HRP-filled neurons was evident, and labelled synaptic terminals of their axon collaterals were easily recognized. Small, dark structures such as ribosomes were completely obscured. The density of the HRP across the injected neurons, and even within a single neuron, varied considerably, probably owing to the amount and site of injected material (compare figures 7 and 8).

Soma and dendrites. The somata were completely thin-sectioned for only two of the neurons (X1 and X2). A cytoplasmic laminar body (c.l.b.; Smith *et al.* 1964; Morales *et al.* 1964; LeVay & Ferster 1977; Kalil & Worden 1978; Schmidt & Hirsch 1980) was present for neuron X1 (figure 4), but not for neuron X2. Therefore, at least some X-cells cannot be distinguished by this cytological feature. For neurons Y1 and Y2, portions of the soma that were not thin-sectioned were serially sectioned at 1 μm, a thickness that permits identification of cytoplasmic laminar bodies at the light microscopic level. Neither of these neurons exhibited such a body.

Description of plate 1

Figure 1. Light photomicrographs of an X-cell (X1) subsequently analysed with the electron microscope. (*a*) Low-power view of coronal section through the lateral geniculate nucleus after osmication and embedding in Epon between two thin pieces of plastic. The neuron is just discernible at the tip of the arrow. (*b*) Higher magnification of the HRP-filled neuron showing the soma and numerous dendrites, both proximal and distal. The white arrow points to a region of dendritic appendages, and the black arrows refer to matching points seen in (*c*). Scale bar = 50 μm. (*c*) A section 1 μm thick showing portions of the soma and dendrites (dark regions). The arrows indicate dendritic segments located by the black arrows in (*b*). The section was stained by the method of Richardson *et al.* (1960). Scale bar = 25 μm.

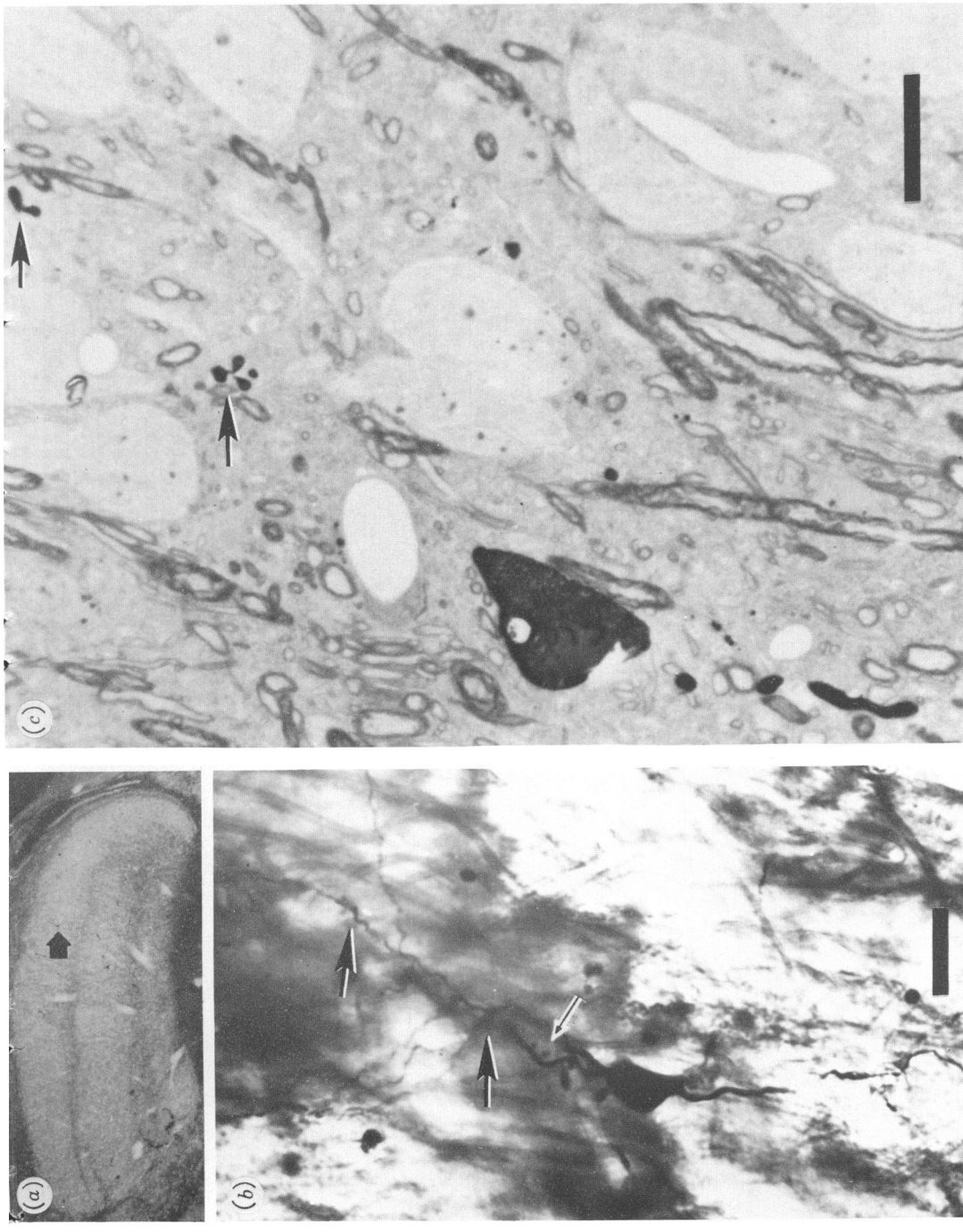

FIGURE 1. For description see opposite.

(*Facing p.* 418)

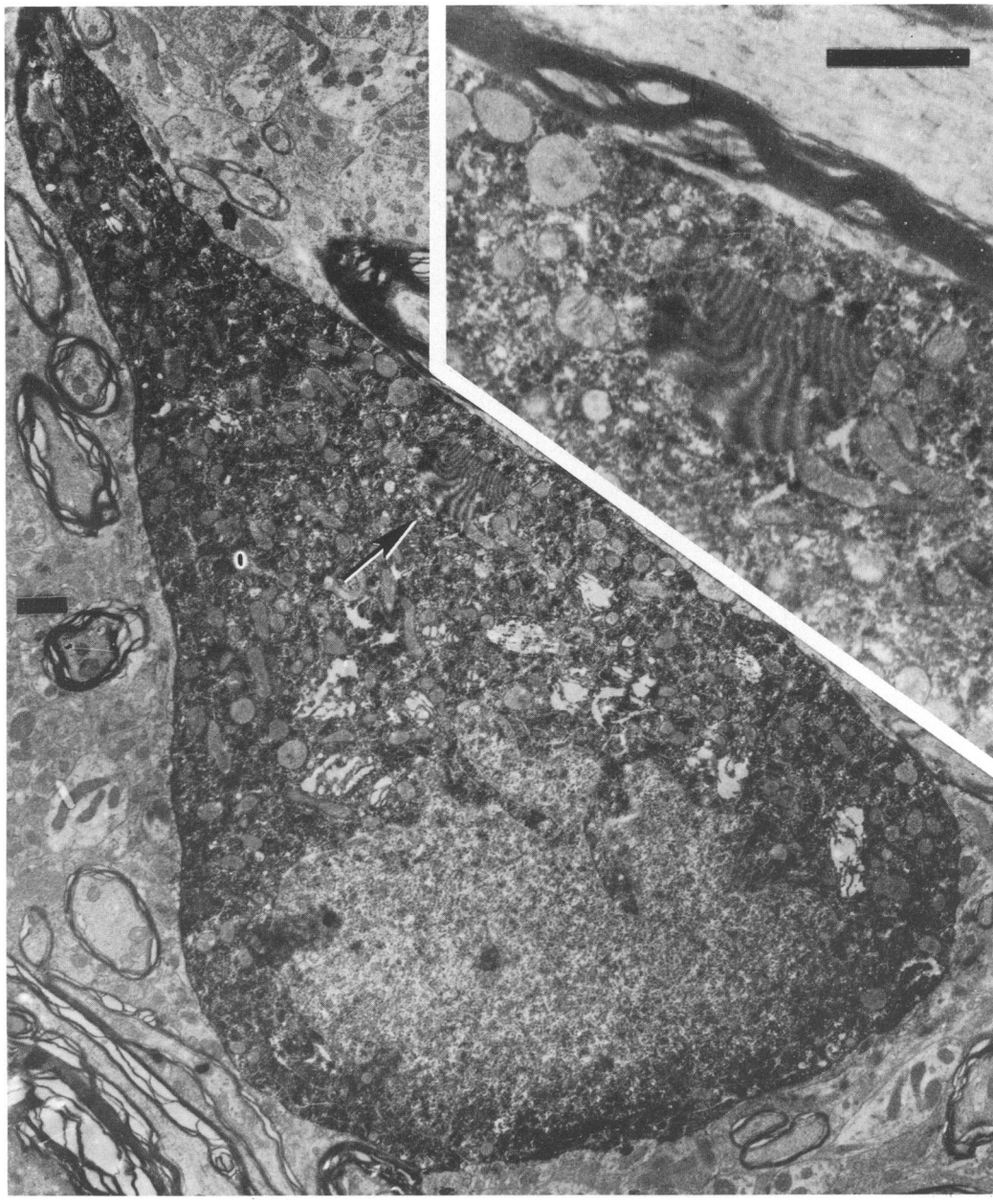

FIGURE 4. Electron microscopic photographs of the same neuron as in figure 1 after thin-sectioning through the soma. Note that the HRP clearly demarcates the neuron by diffusely spreading through most of the non-membraneous spaces. The arrow points to a cytoplasmic laminated body which is further magnified in the inset. Scale bars = 1 μm.

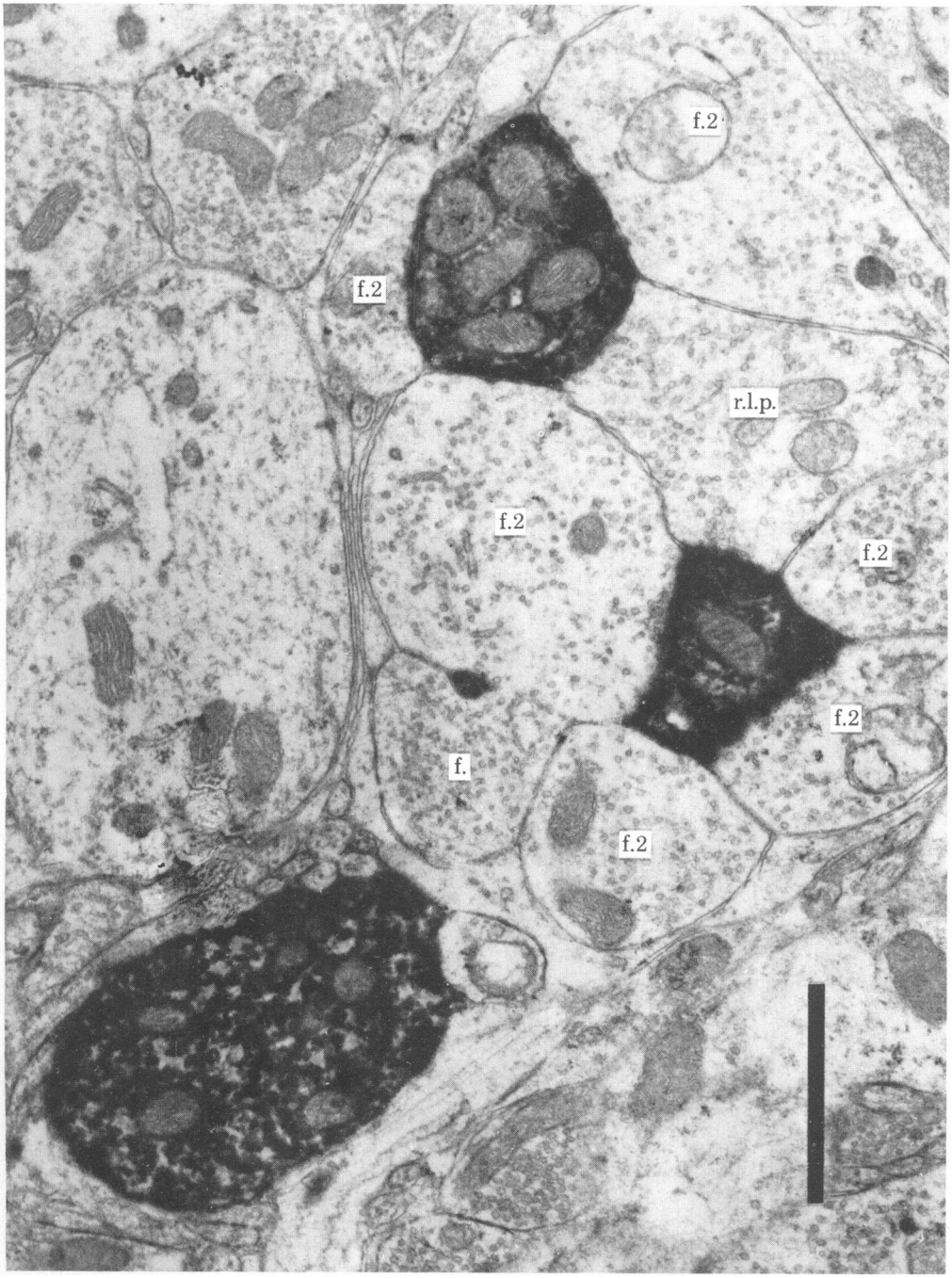

FIGURE 5. Electron photomicrograph of an HRP-filled proximal dendrite (bottom left) and two appendages of an X-cell (X1). This glomerular area of X1 (figure 3*a*, c) shows r.l.p. and f. 2 type terminals surrounding the appendages. An unclassified f. terminal is also present. Scale bar = 1 μm.

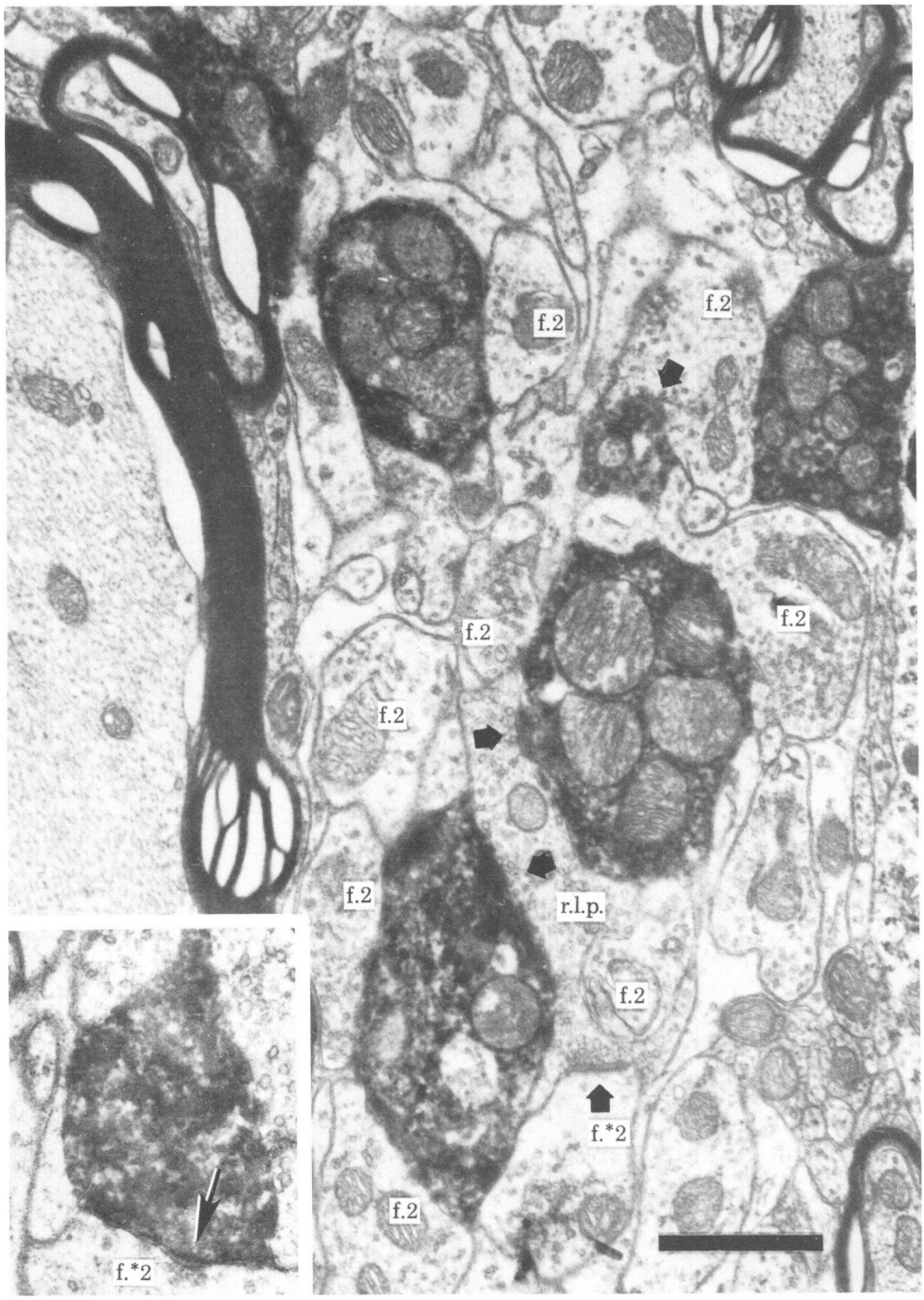

FIGURE 6. R.l.p. and f. 2 type terminals contacting dendritic appendages of cell X2 (figure 3*c*, f). Arrows indicate synaptic contacts of r.l.p. and f. 2 terminals onto the appendages. A triadic arrangement is also shown in this figure with the r.l.p.-f.*2 and r.l.p.-dendrite synapses being indicated by the lower two arrows. The inset, taken from a nearby section, completes the triadic arrangement with the third synapse being made onto the lowest HRP-filled appendage in the main part of the figure. Two other r.l.p.-dendrite synapses are indicated by the upper two arrows. Scale bar = 1 μm.

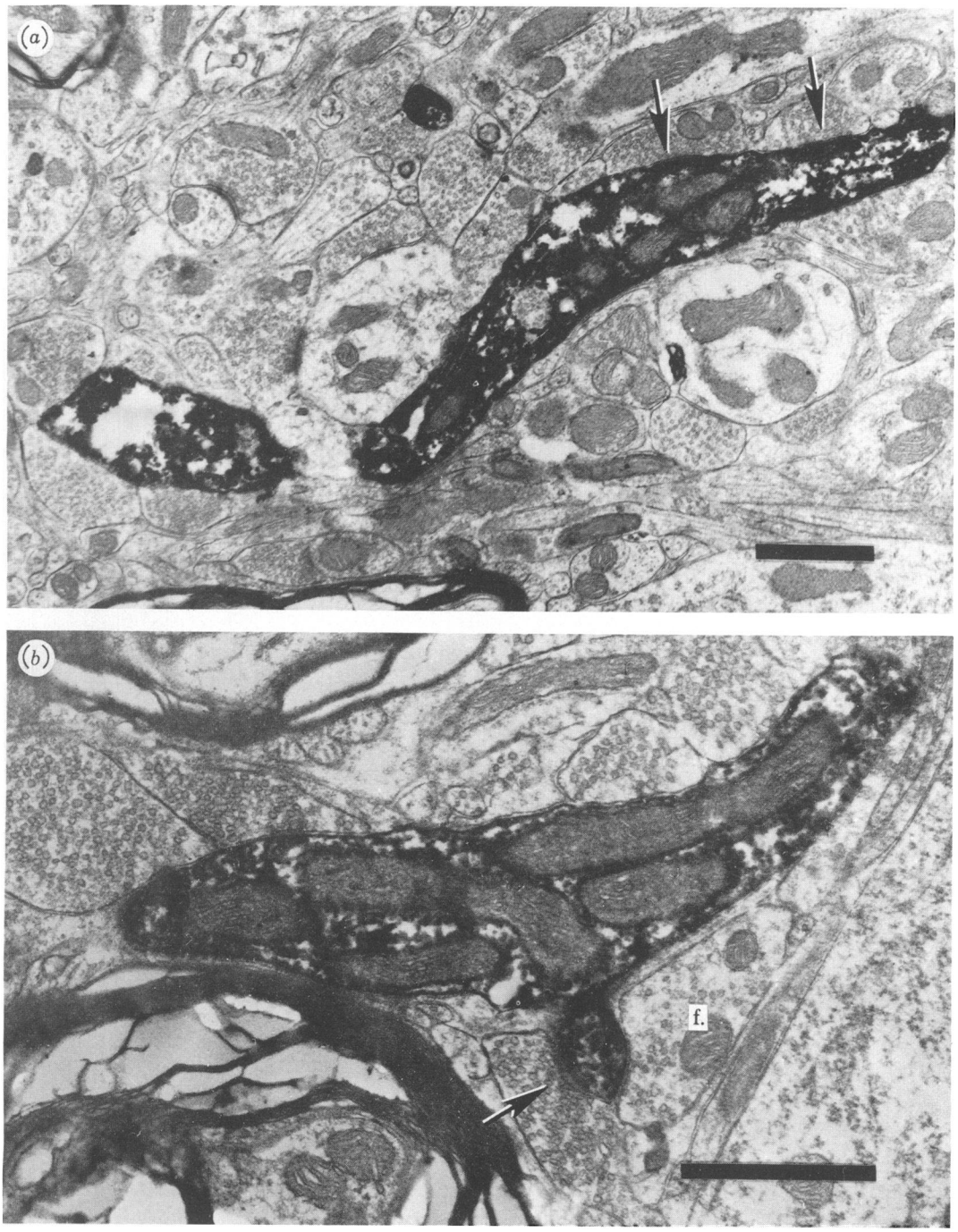

FIGURE 7. HRP-filled dendrites of an X-cell. (*a*) Tangential section through a distal dendrite of X1 showing several synaptic contacts (arrows) by r.s.d. terminals (figure 3*a*, b). (*b*) Another tangential section of a distal dendrite of cell X1 showing an f. terminal and an r.s.d. terminal and synapse (arrow) onto a non-bulbous dendritic appendage (figure 3*a*, h). Scale bars = 1 μm.

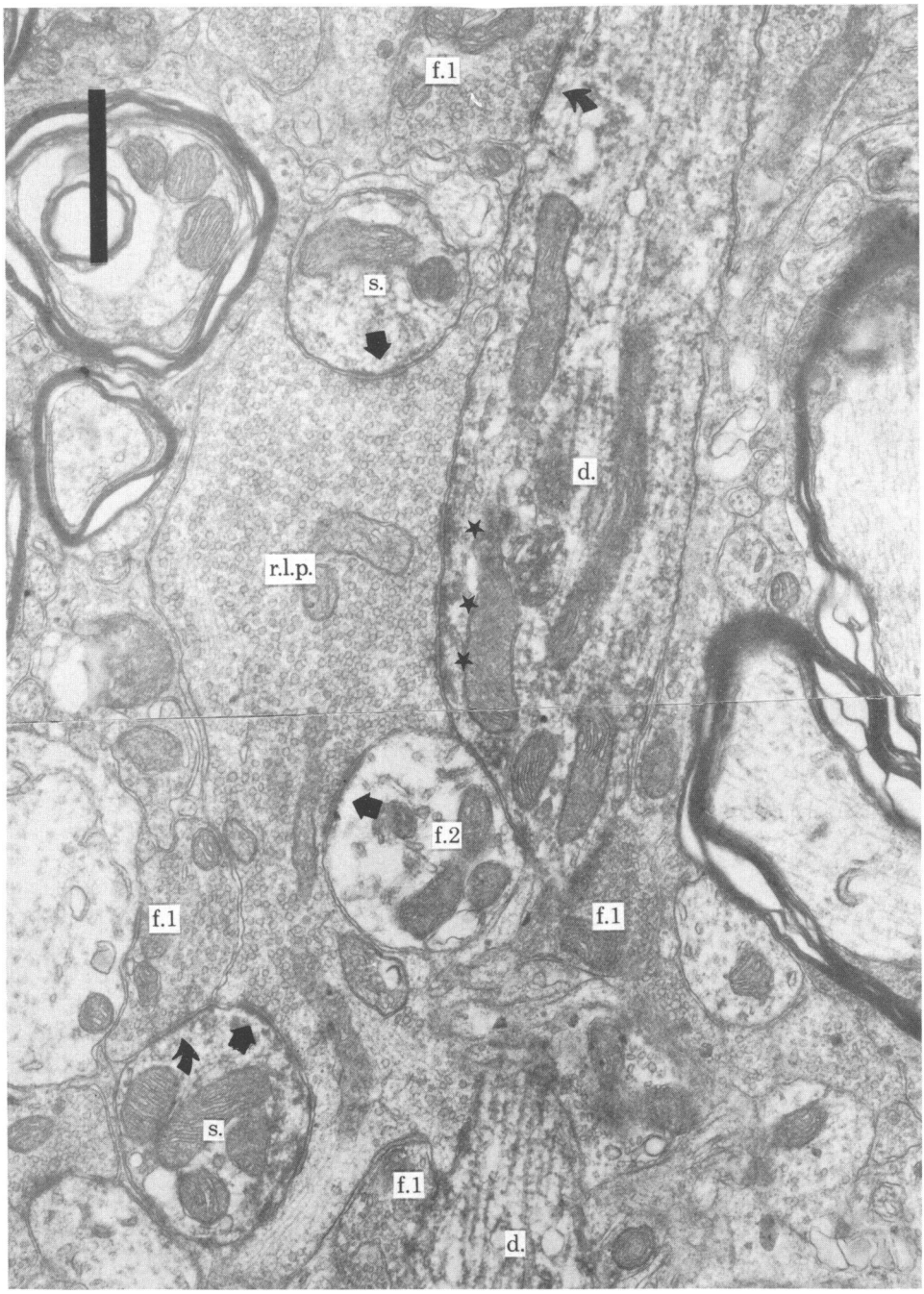

FIGURE 8. Partial tangential section through a proximal dendrite and the heads of two appendages of Y2 (figure 3*d*, m). In further sections, these appendages connected to the main dendrite (*d*). A large r.l.p. terminal is shown attached to the main dendrite at the stars, probably as a punctum adhaerens. This terminal also makes synapses onto the two appendages (s.) and the f. 2 terminal (arrows). Note that the f. 1 terminals and their synapses (curved arrows) are relatively numerous. Scale bar = 1 μm.

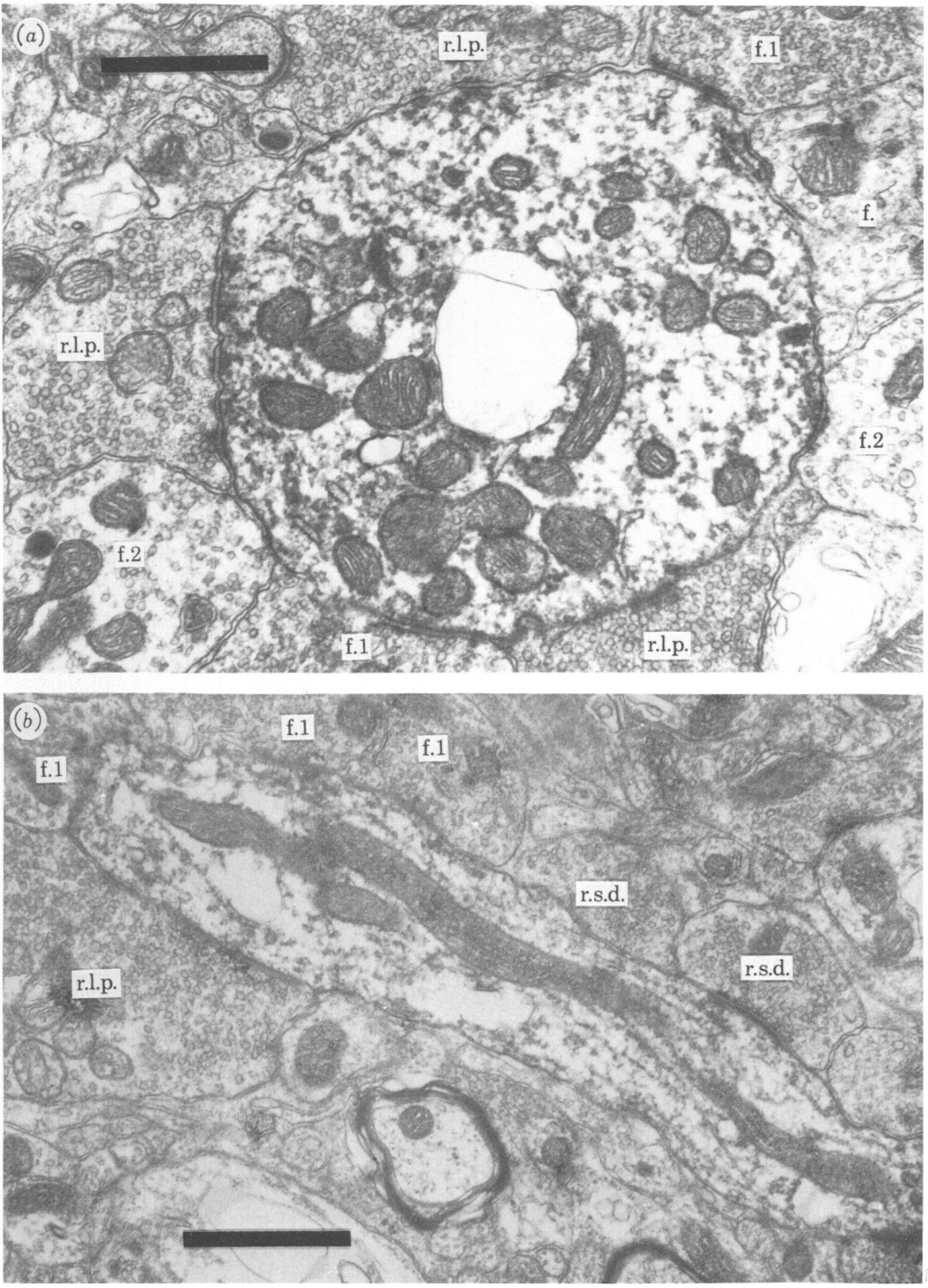

FIGURE 9. Cross-sections through proximal dendrites of a Y-cell (Y2). (*a*) This proximal dendrite is surrounded by r.l.p. and f. terminals that form synapses with it (figure 3*d*, j). (*b*) An r.l.p., three f. 1, and two r.s.d. terminals contact an HRP-filled dendrite of Y2 (figure 3*d*, l). Scale bars = 1 μm.

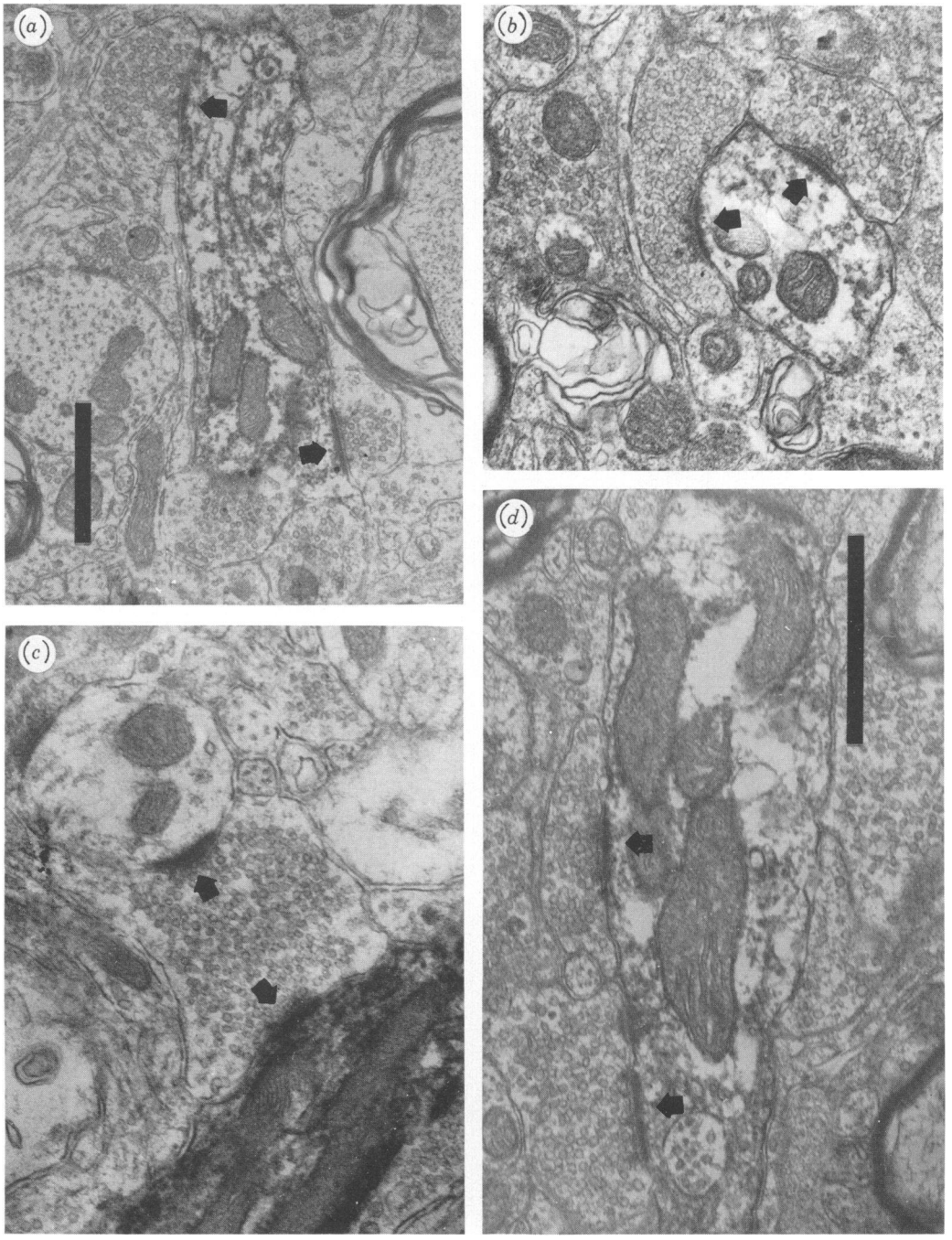

FIGURE 10. Distal dendrites of two Y-cells. Figures (*a*) and (*c*) show r.s.d. terminals contacting cell Y1 (figure 3*b*, d and e). In (*c*) an r.s.d. terminal forms two contacts – one with the HRP-filled dendrite (of Y1) and one on to another dendrite which has no HRP in it. Figures (*b*) and (*d*) show r.s.d. synapses onto two distal dendrites of Y2 (figure 3*d*, i and k). The two densities in the lower part of (*d*) were counted as only one synapse because of their continuity in further sections. Scale bars = 1 μm. Scale bar for (*b*) and (*c*) same as in (*d*).

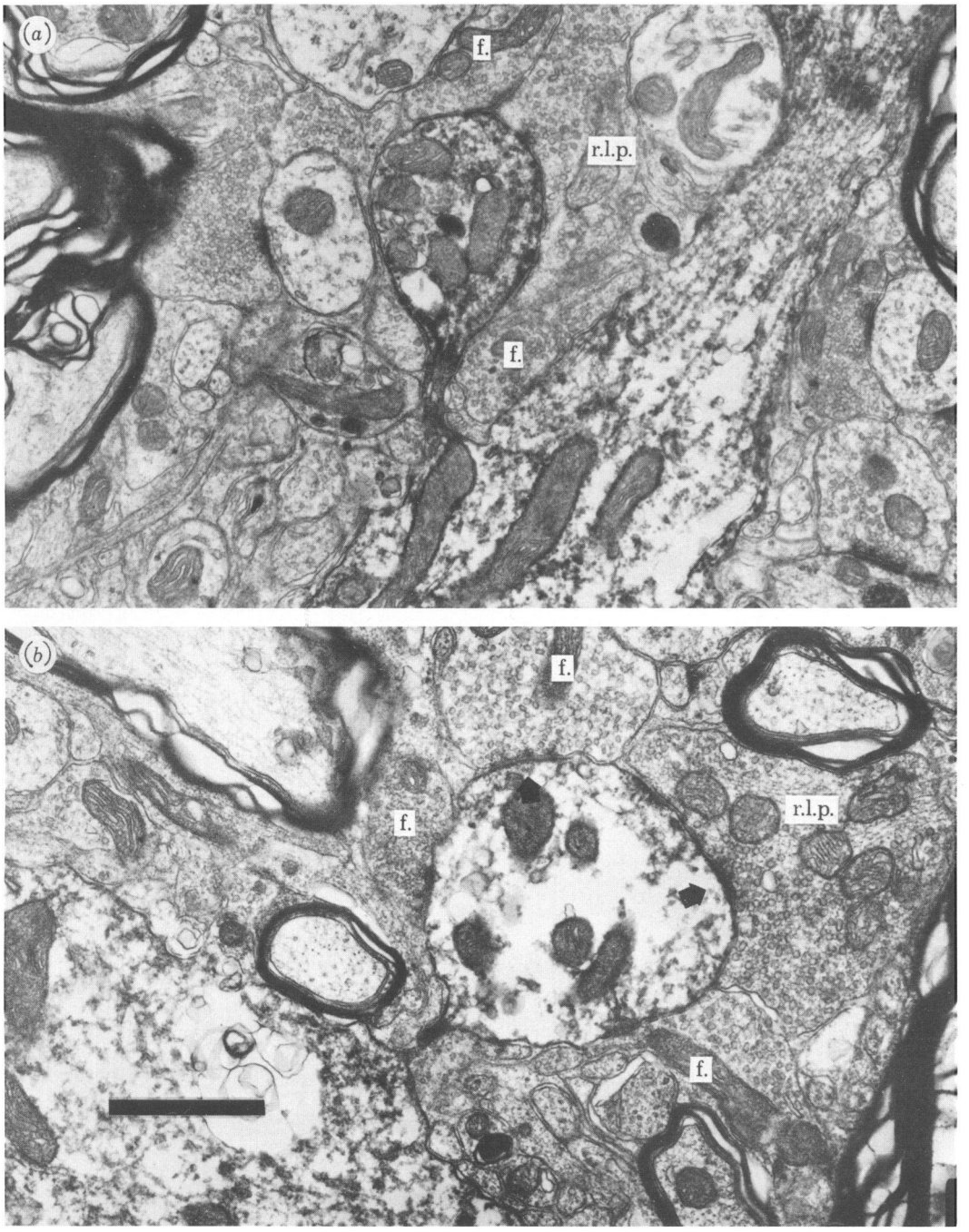

FIGURE 11. Sections through two appendages from Y2 (figure 3*d*, n). These were fortuitous in that the plane of sectioning included the head and neck of each appendage at their widest points. Figures (*a*) and (*b*) show r.l.p. and f. 1 terminals contacting the appendages. Scale bar = 1 μm.

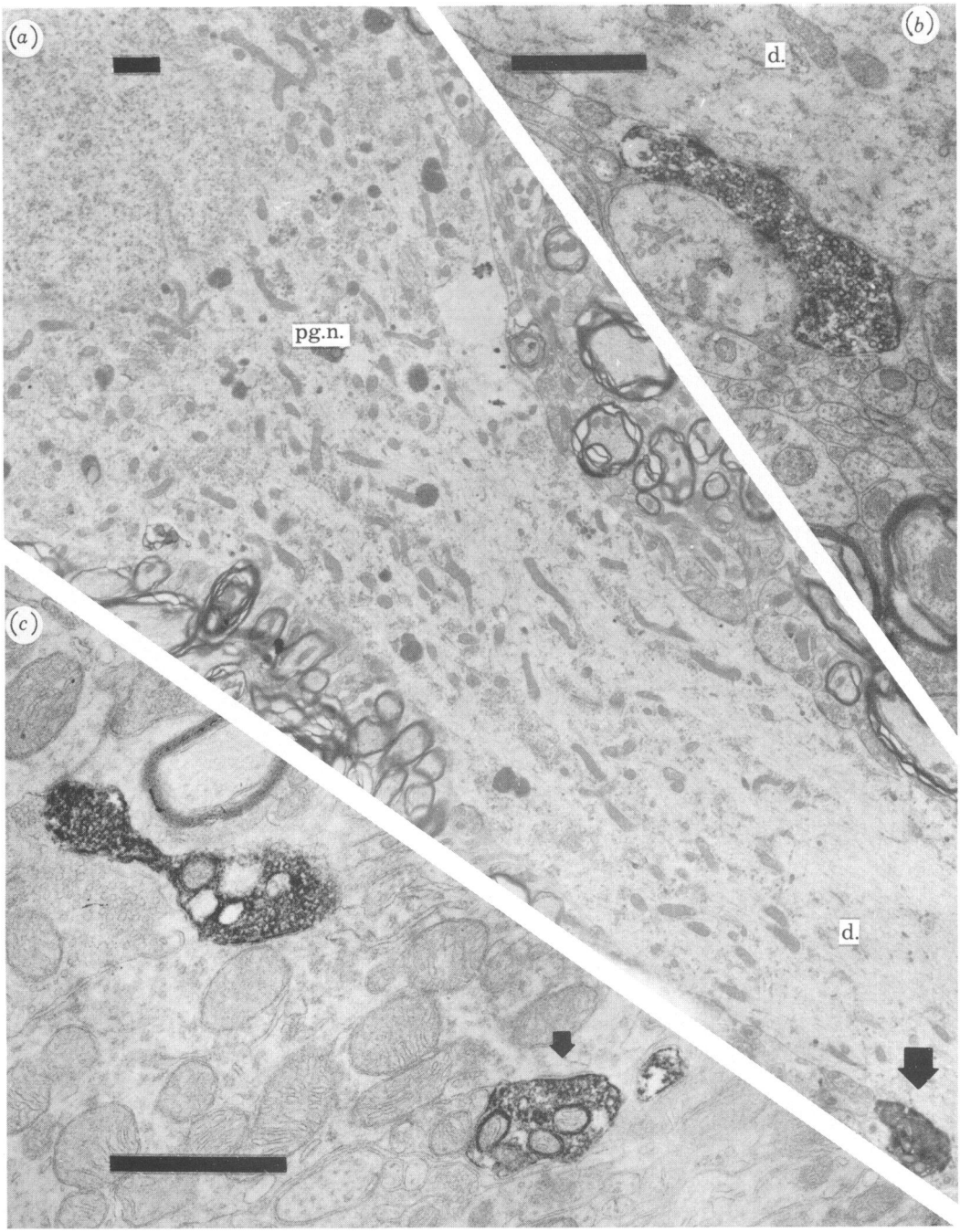

FIGURE 12. Axon collaterals from an X-cell and a Y-cell. (*a*) Neuron in the perigeniculate nucleus which has an HRP-labelled terminal contacting its large proximal dendrite (arrow). This collateral terminal was from the axon of an X-cell (X1; see figure 3*a*, a). (*b*) Higher magnification of the same terminal contacting the dendrite, but from a separate, nearby section. Note that round synaptic vesicles are clearly evident. (*c*) An intrageniculate axon collateral from a Y-cell (see text). Axon appears to have an *en passant* synapse (arrow) onto a dendrite which was located in lamina A. Scale bars = 1 μm.

Except for the single cytoplasmic laminar body in X1, the cytoplasmic morphology of the somata and dendrites was indistinguishable among all four neurons. Also, despite close scrutiny, no qualitative difference was evident for any of the terminals with round vesicles and asymmetrical synapses contacting the HRP-filled dendrites. In particular, the profiles of the retinal terminals did not show any qualitatively distinctive features that would allow a differentiation between X- and Y-cell optic tract terminals. However, there was a difference between the terminals having flattened or pleomorphic vesicles which contacted X-cells compared to those that contacted Y-cells (see Triadic arrangements below). None of these four neurons exhibited characteristics of presynaptic dendrites (compare Famiglietti 1970; Lieberman 1973). The visibility of synaptic vesicles in terminals of axon collaterals from injected cells (figure 12) demonstrated that synaptic vesicles would have been seen if present, but no such vesicles were observed in any HRP-filled dendrite.

Synaptic types. Terminal or vesicular profile types were recognized by their characteristic morphology. The nomenclature proposed by Guillery (1969) will be used in this study. Briefly, r.l.p. terminals are retinal in origin (Szentágothai *et al.* 1966; Jones & Powell 1969; Guillery 1969; Hendrickson 1969; Robson & Mason 1979). They have *r*ound synaptic vesicles, are relatively *l*arge, and contain many *p*ale mitochondria (figures 5, 6, 8 and 9). The r.s.d. terminals (many originating from the cortex, see Discussion) also have *r*ound synaptic vesicles, but the terminals are relatively *s*mall and sometimes contain *d*ark mitochondria (figures 7 and 10). The r.l.p. and r.s.d. terminals make asymmetrical synaptic contacts. The f. terminals are characterized by *f*lattened or pleomorphic synaptic vesicles and symmetrical synaptic contacts (figures 5, 6, 8 and 9). Many of these terminals are undoubtedly from intrathalamic sources (Szentágothai *et al.* 1966; Famiglietti 1970; Guillery 1971; Famiglietti & Peters 1972; Lieberman 1973; Rafols & Valverde 1973; Pasik *et al.* 1976; Montero & Scott 1981). The f. terminals can be further subdivided into f. 1 and f. 2 types (Guillery 1969; Wong 1970; LeVay 1971; Famiglietti & Peters 1972; Winfield *et al.* 1980). Compared to f. 2 terminals, f. 1 terminals typically have a darker cytoplasmic matrix and more flattened synaptic vesicles that fill the profile. In an f. 2 terminal, the synaptic vesicles have more irregular shapes and sizes (pleomorphic), sometimes clustered in only one area of the profile, and reside in a lighter cytoplasmic matrix. However, there are many f. terminals that cannot clearly be distinguished as an f. 1 or f. 2 type terminal (Guillery 1969). Our classification and conclusions for f. 1 and f. 2 terminals are based on the majority of f. terminals that can be placed into one of these categories. The main distinguishing features for our material were the lighter cytoplasmic matrix and fewer vesicles for the f. 2 terminals. These three terminal types – r.l.p., r.s.d., and f. – constitute over 95% of all the terminals seen in the A laminae of the lateral geniculate nucleus, and they were the *only* types seen making synapses onto the HRP-filled neurons.

Synaptic contacts. For each of these neurons, every proximal dendritic appendage studied was postsynaptic to an r.l.p. terminal and often to an f. terminal as well (figure 11). The large majority of these appendages were located within 100 μm of the centre of the soma at dendritic branch points. Occasionally more distal

bulbous appendages were observed, and they also received similar synapses. An example of a non-bulbous appendage is shown in figure 7*b*. This appendage was on a distal dendrite and did not receive an r.l.p. synapse. It did receive an r.s.d. synapse and an f. synapse. The distal dendrites ventral to the soma of neuron X1 had many appendages, but unfortunately these were not processed for electron microscopy.

For the two X-cells, nearly all r.l.p. terminals contacted dendritic appendages. Very few dendritic appendages were present on the two Y-cells, and most of these were located near or at the branch points of proximal dendrites. These few appendages of the Y-cells were always contacted by retinal terminals. Figure 8 shows a single r.l.p. terminal contacting two separate dendritic appendages for Y2. The r.l.p. terminals onto the two Y-cells were not confined to appendages as was the case for the two X-cells; in fact, most of the r.l.p. synapses were made onto the main dendrites (figure 9). Nearly all of the r.l.p. synapses made onto Y1 and Y2 were located near the proximal branch points either on appendages or the main dendrites themselves. Y1 had branch points very close to the soma (< 20 μm) and Y2, although its branch points were further out, had numerous r.l.p. synapses before these points. There were no retinal terminals observed on either Y-cell that were further than 75 μm from the edge of the soma.

The f. terminals concentrated near the retinal terminals (figures 5, 6, 8 and 9) and were sparser on the distal dendrites for all four neurons. In fact, the f. terminals usually abutted the r.l.p. terminals. For the X-cells, the majority of the terminals were of the f. 2 type. Many of these f. 2 terminals also received synapses from the retinal terminals (figures 5 and 6) and participated in triadic arrangements (see also below). The Y-cells, on the other hand, had a large number of f. 1 terminals (figures 8 and 9), and these did not receive r.l.p. contacts. Some f. 2 terminals were also observed which did not participate in a triadic arrangement.

The r.s.d. terminals clearly predominated on the distal dendrites (figures 7 and 10), although they were also seen on more proximal dendrites. (see Quantitative observations below). Figure 10*c* illustrates an r.s.d. terminal contacting both a labelled and an unlabelled dendrite. This indicates that some of these axons are not restricted to a single geniculate neuron within a lamina.

Axon collaterals. Geniculate relay cells frequently send branches or collaterals of their axons into the perigeniculate nucleus (Jones 1975; Ferster & LeVay 1978; Ahlsén *et al.* 1978; Friedlander *et al.* 1981; Stanford *et al.* 1983). On the other hand, collaterals that terminate within laminae A or A1 are less frequent (Ahlsén & Lindström 1978; Friedlander *et al.* 1981; Stanford *et al.* 1983). We have briefly examined one example of each type of collateral from separate neurons. The collateral from neuron X1 projecting into the perigeniculate nucleus is illustrated in figure 12. The terminal makes contact with a large proximal dendrite of a perigeniculate neuron (figure 12*a*). It can be seen that this collateral has round vesicles which are closely packed together (figure 12*b*).

The collateral terminating within lamina A originated from a cell that has not yet been otherwise analysed. This neuron was a Y-cell in the non-deprived lamina A of a monocularly lid-sutured cat. Figure 12*c* illustrates the fine structural morphology of this terminal. This terminal, like the terminal observed in the

perigeniculate neuron, also had round synaptic vesicles which were closely packed together. Despite coming from different cell classes, the appearance of the perigeniculate and intrageniculate collateral terminals described here are very similar and resemble r.s.d. terminals (but see Ide 1982).

Quantitative observations

Although the selected tissue was serially sectioned and stored, no attempt was made to reconstruct any parts of the neuron except in the cases noted below. That is, our principal aim was to determine the types, positions and relative number of synaptic complexes made on to the neuron rather than a complete count of all synapses. However, we did attempt to estimate this total number for two of the cells (X2 and Y2).

The first two neurons that we studied (X1 and Y1) were examined less systematically in order to obtain a rapid overview of their fine structural features. None the less, the data gathered from these cells, particularly in terms of percentages of synaptic types at various locations along the dendrites, were very similar to those of the second, more systematically examined, X- and Y-cell (X2 and Y2). The results of the analyses will be presented below in two ways. First, the relative number of each synaptic type at various distances away from the centre of the soma will be presented for all four neurons (X1, X2, Y1, Y2). Second, the data from cells X2 and Y2 will be used to obtain estimates of the *total* number, type and distribution of terminals made onto the entire dendritic arbor.

Relative distribution of synaptic types. Figure 13 shows the percentages of synapses from r.l.p., r.s.d., and f. terminals made onto the dendrites of each of the four neurons at increasing distances from the centre of the soma. An estimated total number or density of synapses could not be determined for X1 and Y1 owing to the less systematic sampling for these cells as noted above. The distance between each terminal and the centre of the soma was estimated by centring around the soma a series of concentric circles 50 μm apart and determining which annulus contained the terminal being studied. Two qualifications to these measurements must be noted. First, these distances are taken from the centre of the soma; the edge of the soma would be roughly 10–15 μm closer to the synapses. Second, the actual conduction path along a dendrite departs from a straight line, particularly for a more peripheral location with several branch points between it and the soma. The values of figure 13 may thus underestimate actual distances along dendrites. However, a vast majority of the dendrites were radially oriented away from the soma (figure 2), so that the distance along the dendrite would also be reasonably close to the radial distance for the 50 μm sections selected for fine structural examination (see also table 3 footnote).

From figure 13, it is clear that r.s.d. terminals, although they were numerically few (see figure 14), predominated on the distal dendrites (up to 90 % of the total synapses in the region), but were rare (as low as 3 %) very close to the soma. Overall, r.l.p. and f. terminals were relatively numerous near the soma and became less frequent at increasing distances along the dendrites. However, the X-cell and Y-cells differed in their relative ratios of r.l.p. and f. terminals. Within 100 μm of the centre of the somata, the two Y-cells had approximately equal percentages of f. and r.l.p.

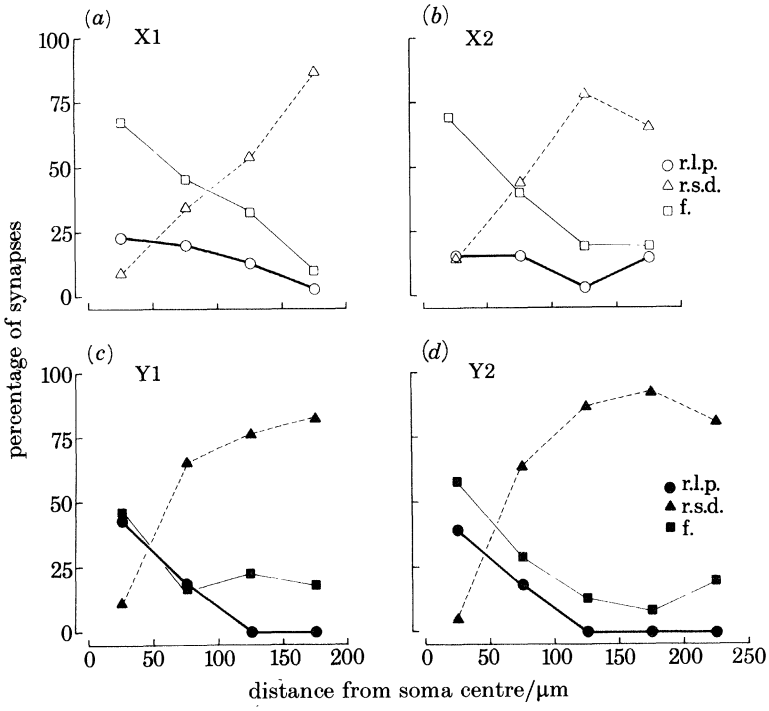

FIGURE 13. Graphs of the percentage of each terminal type (r.l.p., r.s.d., f.) making a synapse on to the dendrites of the four cells studied. The abscissa gives the distance of the synapses from the centre of the soma for each cell. The ordinate value of each point was calculated by dividing the number of synapses of that type by the total of all of the synapses within each 50 μm annulus. Note that all four neurons have similar distributions of synaptic terminals onto their dendrites although the Y-cells tend to have a higher percentage of r.l.p. terminals (near the soma) than do the X-cells.

terminals, but the X-cells had at least three times as many f. as r.l.p. terminals. For the Y-cells, there were no retinal terminals seen beyond 100 μm of the centre of the soma. A few retinal terminals were seen onto peripheral appendages of the X-cells.

Although the f. terminals were especially numerous (up to 68% of the total synapses) near the areas where the retinal terminals formed synapses, the f. terminals also contributed a reasonable fraction (10–20%) of the total synapses on the distal dendrites where few or no retinal terminals were present. As previously mentioned, a major qualitative difference seen between the X- and Y-cells was the large number of f. 2 type terminals associated with the X-cells compared to the Y-cells (see figures 5, 6, 8 and 9). Although we did not quantify the different f. terminal populations, the f. 2 terminals for the X-cells appeared to be concentrated on the proximal dendrites, whereas the f. 1 terminals were much less frequent and distributed rather randomly throughout the dendritic arbors. The Y-cells had many more f. 1 terminals associated with their dendritic arbors than the X-cells. As discussed below, the difference in the types of f. terminals making contacts with X-cells and Y-cells seem to be intimately related to the presence of many triads and appendages for the X-cells.

Triadic arrangements. A triadic complex in the lateral geniculate nucleus is composed of a presynaptic terminal (usually an r.l.p.) that forms synapses upon both an f. terminal and a dendrite, and the f. terminal also forms a synapse onto the same dendrite (Colonnier & Guillery 1964; Jones & Powell 1969; Hámori *et al.* 1974; Rapisardi & Miles 1984; Lieberman & Webster 1974). In this paper, a further qualification for a triadic arrangement was that each synapse could participate in only one triad, and all three synapses were required to be within a reasonable distance of each other (about 2–3 μm). Such triads are not frequently observed in single thin sections because the plane of section rarely passes through all three synapses, but several were observed for cell X1. The serially reconstructed lengths of dendrites for neurons X2 and Y2 (figure 3, brackets) permitted us to observe all of the total synaptic arrangements within these areas. Specific attention was given to possible triadic arrangements. No triadic arrangements were seen for any of the r.s.d. terminals. For cell Y2, only one triadic arrangement was observed out of 15 r.l.p. terminals that contacted the proximal, reconstructed dendrite. This reconstruction extended 38 μm and included a branch point plus two appendages. No triadic arrangement was observed in any other section of either cell Y1 or Y2, proximally or distally. In contrast, the serial reconstruction (29 μm) of a proximal dendrite of X2 revealed eight triads out of nine r.l.p. terminals presynaptic to the dendritic appendages. Therefore, it was quite clear that the X-cells differed from the Y-cells in commonly exhibiting triadic arrangements as part of their retinogeniculate circuitry.

Another important feature of the triadic arrangement was the type of f. terminal involved. Only f. 2 terminals were involved with triads, both for the X-cells and for the single triadic arrangement seen for cell Y2. The f. 1 terminals did not participate in any triadic arrangements. The f. 2 terminals receiving the r.l.p. synapse did not always contact the same appendage receiving the r.l.p. terminal. Instead, the f. 2 terminals sometimes formed a synapse onto either the main dendritic shaft or onto the head of another appendage (figure 6).

Estimated total number and distribution of synapses. For the second X- and Y-cell that we analysed (cells X2 and Y2), a more systematic approach was made to determine the total afferent inputs to their dendrites. To avoid the extremely time-consuming process of serially reconstructing the entire dendritic arborizations of the neurons, a more practical approach was used which consisted of three steps. (i) After we selected the 50 μm thick Epon section(s) from which to obtain our thin sections, we serially thin-sectioned the trimmed block and closely examined every tenth thin section under the electron microscope. Each terminal having a synapse with the HRP-filled dendrites was photographed (at 10000–15000 × and printed at 20000–30000 ×), classified, counted, and its position on the dendritic arbor noted. By this method, we obtained the type and position of the terminals on to a specified amount of dendritic material (table 2). (ii) Serial reconstructions were made of a length of one distal (54 μm) and one proximal dendrite (38 μm) from cell Y2 (see figure 3, brackets). Reconstructions were also carried out for X2 through one of its proximal dendrites (29 μm) including a 'grape-like' cluster. These serial reconstructions permitted us to estimate the error caused by using every tenth thin section for our counts rather than total serial reconstructions. That is, large synapses (for example, from r.l.p. terminals) might be overestimated

because they extended through more than ten thin sections (that is, they would be counted more than once), whereas small synapses (for example, from r.s.d. terminals) might be underestimated because many of them might lie in tissue between the sampled thin sections (that is, they would not be counted at all). The correction factors for these sampling errors were derived by dividing the actual number of synapses of that type on the reconstructed dendritic length by the

TABLE 2. SYNAPTIC COUNTS ACTUALLY MADE FOR NEURONS Y2 AND X2. THE ESTIMATED TOTAL SYNAPTIC COUNTS AND DISTRIBUTIONS OF FIGURE 14 WERE DERIVED FROM THESE NUMBERS

distance from soma centre/μm ...	0–50	51–100	101–150	151–200	201–250	total counts
			Y2			
r.l.p.	32	28	0	0	0	60
r.s.d.	3	82	45	20	9	159
f.	50	44	8	2	2	105
						325
			X2			
r.l.p.	15	21	1	5	0	42
r.s.d.	6	68	30	25	0	129
f.	64	60	7	7	0	138
						309

TABLE 3. DENDRITIC LENGTHS†

distance from soma centre/μm ...	0–50	51–100	101–150	151–200	201–250	total
sectioned						
X1	82	353	388	117	0	940
X2	171	118	140	130	5	564
Y1	144	409	845	921	0	2319
Y2	125	192	188	79	29	613
total						
X1	671	1373	1579	558	33	4214
X2	1204	1682	855	283	38	4062
Y1	1362	4073	5768	3014	948	15165
Y2	1385	2521	1658	730	94	6388

† Measurements of the dendritic lengths (in micrometres) were estimated from two-dimensional drawings of these three-dimensional structures. Exceptions to this were made for the 50 μm thick sections used for quantitative synaptic counts. In these cases, any vertical or near-vertical dendrites were directly measured by using the plane of focus of the microscope and the calibrated focusing knob. Because the other dendrites in the remaining sections of each cell were not directly measured under the microscope, many of their dendritic lengths would have been underestimated. For the spherical or hemispherical Y-cells, the average angle out of the plane of section for a dendrite would have been 45 deg and the sine of this angle (0.71) would be the measured distance on a two-dimensional drawing (that is, a 29% underestimation of the true lengths). Therefore, we have divided all of the measured lengths for Y1 and Y2 by 0.71 to correct for this factor. This error would be less for the X-cells owing to their non-spherical dendritic arbors and our plane of section being near parallel to the directional spread of their arbors (estimated error about 8%, so measured lengths were divided by 0.92 to obtain the values in the table).

number obtained along that same dendritic length using every tenth thin section. The calculated values were as follows: r.l.p., 17/20 = 0.85; f., 67/45 = 1.49; r.s.d., 78/51 = 1.53. Therefore, r.l.p. synapses were overestimated by about 20%, but f. and r.s.d. synapses were underestimated by about 30%. (iii) The lengths of the dendrites from which we obtained our synaptic counts (that is, the length of *sectioned* dendrites within each 50 μm annulus) were measured. Also, the total length of all dendrites, sectioned and unsectioned, within each 50 μm annulus was measured (table 3). The synaptic counts were then corrected for each 50 μm annulus by using a multiplication factor derived by dividing the total dendritic length by the sectioned dendritic length. Figure 14 shows the estimates made for the total synaptic inputs to one X-cell and one Y-cell. A sample calculation for one of the estimates is given in the legend of figure 14.

Several conclusions can be drawn from figure 14. First, the total estimated number of synapses made onto both neurons is similar (about 4000 for cell X2 versus about 5000 for cell Y2). Compared to cell X2, cell Y2 has 72% more r.l.p. synapses, 38% more r.s.d. synapses, and 10% fewer f. synapses. Second, within 50 μm of the soma centre, the number of retinal synapses for cell Y2 is three to four times the number for cell X2, and there are few (cell X2) or no (cell Y2) r.l.p. synapses beyond 100 μm from the centre of the soma. Third, although in a relative sense the r.s.d. synapses are the most common type found on the distal dendrites (beyond 100 μm), none the less, there are more r.s.d. synapses found between 50–100 μm from the soma centre than distally. Fourth, f. synapses are present even on the distal dendrites where retinal synapses are scarce, but are clearly the most common synapses type nearer the soma. Qualitatively, we observed that the f. synapses were mostly located near the r.l.p. synapses.

Density of synapses. The total number of synapses is an important parameter concerning the afferent input to a neuron, but the density of terminals onto the dendrites at various locations may be of equal or greater importance. For each terminal type, figure 15 shows the estimated density of synapses (synapses per unit length) for each synaptic type as a function of distance from the soma centre. The combined total dendritic tree length was 6388 μm for cell Y2 and 4062 μm for cell X2. The average number of synapses of any type per micrometre of dendritic length was about 0.9 for cell Y2 and about 1.0 for cell X2. The majority of these terminals made synapses in the region 50–150 μm from the centre of the soma, which is also the region that contains most of the dendritic length. Nevertheless, the density of synapses is also highest in this area (1.9 μm^{-1} for cell X2 and 1.1 μm^{-1} for cell Y2). Beyond about 100 μm from the centre of the soma, the amount of dendrites decreases, but the number of synapses has dropped even more such that the density reduces to a fairly constant number of approximately 0.4 synapses per micrometre of dendritic length.

Discussion

Our fine structural observations from two X-cells and two Y-cells within the A laminae of the lateral geniculate nucleus have shown that there are many similarities among these neurons. Although the entire dendritic arbors were not

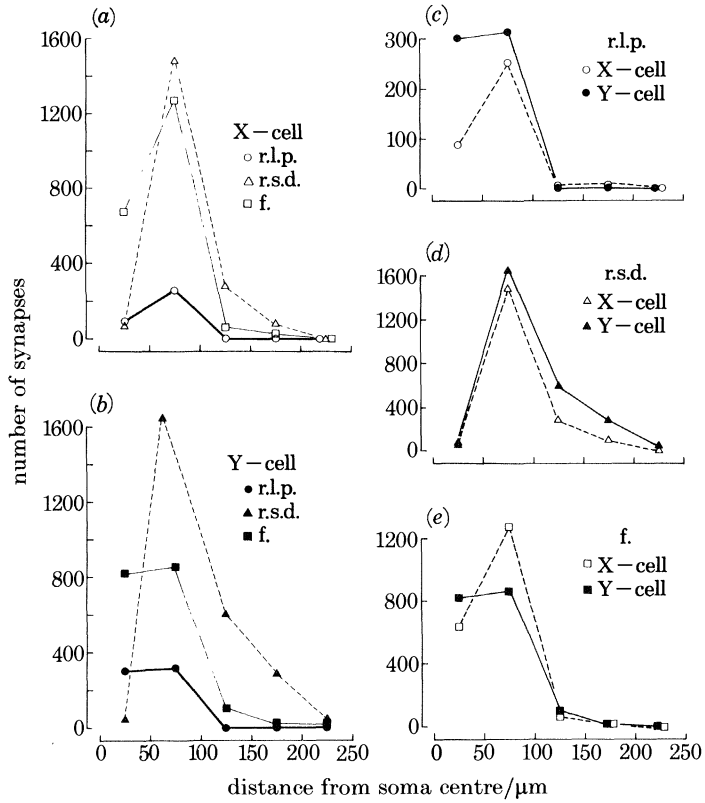

FIGURE 14. Graphs of total estimated number of synapses being made onto the dendrites of an X-cell (X2) and a Y-cell (Y2) as a function of distance from the centre of the soma. To derive these estimates, actual counts from table 2 were multiplied by the appropriate correction factor (see Results section entitled Estimated number and distribution of terminal types) and then adjusted for the total dendritic length within each 50 μm annulus (from table 3). For example, 45 r.s.d. synapses (table 2) were counted from 188 μm of sectioned dendrite (table 3) for Y2 in the 101–150 annulus. The adjustment for using every tenth thin section instead of serial reconstructions was 1.53. The corrected total dendritic length for this annulus was 1658 μm. The adjustment for total r.s.d. synapses on all of the dendrites in this annulus would be 1658/188 = 8.82. Therefore, the 45 r.s.d. counts were multiplied by correction factors of 1.53 and 8.82 to give a total of 607 estimated r.s.d. synapses along the dendrites of Y2 between 101–150 μm from the soma centre. (*a*) and (*b*) Comparisons of all three terminal types for each cell. (*c*), (*d*) and (*e*) Separate comparisons between the X- and Y-cell for each terminal type.

sampled, we believe that the observations are representative for each entire neuron because of their general consistency. This is particularly true for the cytological morphology and synaptic percentages. However, there are also some striking differences in the distributions of the terminals near regions of the retinal synapses: triads and f. 2 type terminals are common in these regions for the X-cells, but rare for the Y-cells. These morphological differences indicate that the retinal signals are processed in a distinctly different manner by X- and Y-cells.

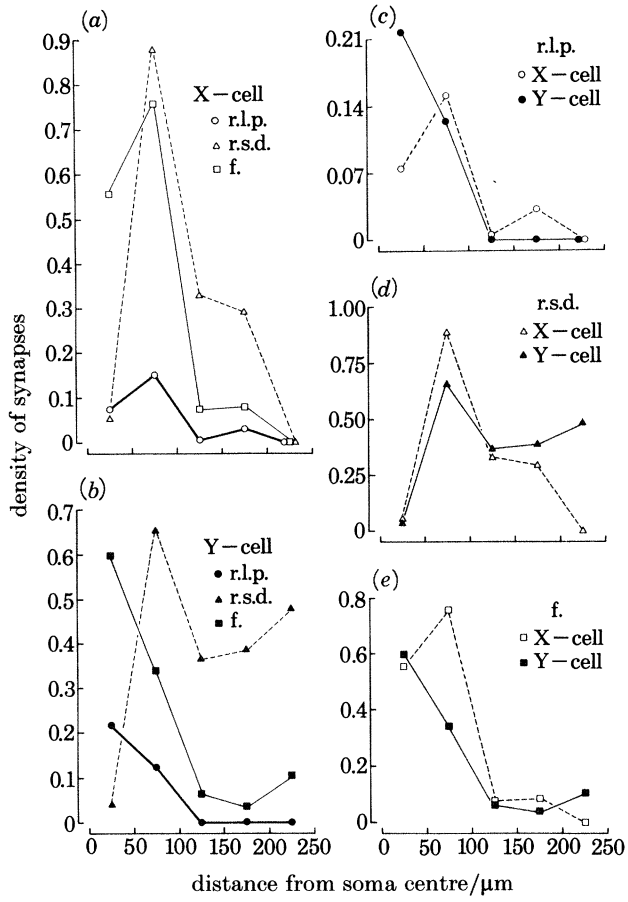

FIGURE 15. Graphs of the density (number per micrometre of dendritic length) of each synaptic type (r.l.p., r.s.d., f.) as a function of distance from the centre of the soma. The points were derived simply by dividing the estimated number of each type within each 50 μm annulus (figure 13) by the total dendritic length for that annulus (table 3). (*a*) and (*b*) Comparisons of all three terminal types for each cell. (*c*), (*d*) and (*e*) Separate comparisons between the X- and Y-cell for each type of synapse.

Synaptic inputs

Relative percentages

Previous investigators who have examined the percentages of different terminal types within the neuropil of the lateral geniculate nucleus (cat: Guillery 1969; monkey: Wong-Riley 1972; Wilson & Hendrickson 1981) found that 15–20 % of all terminals were retinal (r.l.p.), 30–40 % had pleomorphic or flattened vesicles (f) and about 40–50 % were r.s.d. type terminals. Our data from four individually analysed neurons show that each of these neurons has relative numbers of these terminal types that are in fair agreement with these previous studies. That is, when all of the terminals of each type on each of our neurons are considered without regard to their dendritic position, their relative numbers are representative of those

in the surrounding tissue. However, it is quite clear that the distribution of terminal types is not uniform along the dendrites of single neurons. The f. terminals predominate close to the soma, while r.s.d. terminals are the major type on the intermediate and distal dendrites. Guillery (1969) reached a similar conclusion on the basis of the diameters of the postsynaptic dendritic elements.

R.l.p. terminals

R.l.p. terminals are not very numerous anywhere on the dendritic arbor, but they are concentrated near the proximal branch points, which are also where many dendritic appendages often occur. Thus, three of the striking features of the synaptic distributions are the relatively small number of contacts made onto each neuron by retinal terminals, their proximal location within the dendritic arbor, and their selective contact with appendages, particularly for X-cells. Clearly from other physiological evidence the retinal terminals are particularly potent inputs to these neurons. Although these terminals are a minority of the total synapses, it seems safe to assume that their locations near the soma helps them to dominate the firing pattern of the neurons. For the two Y-cells, the r.l.p. terminals do not even extend beyond 100 μm from the centre of the soma, and this means that total dendritic spread cannot correspond with the distance of retinal afferent sampling. This also means that the dendrites that cross laminar boundaries (from Y-cells) are unlikely to be activated by retinal afferents from the opposite eye. Most of the synapses on the distal dendrites are of the r.s.d. type and are probably from cortex, and because single axons from cortex ramify across laminar borders (Guillery 1966, 1967; Tömböl 1966; Szentágothai 1973; Robson 1983), the significance, if any, of any dendrite crossing into another lamina is obscure.

F. terminals

These synaptic profiles are believed by many to mediate inhibitory responses in the lateral geniculate nucleus (Famiglietti 1970; Famiglietti & Peters 1972; Pasik *et al.* 1973; Hámori *et al.* 1974; Pasik *et al.* 1976; Sterling & Davis 1980; Montero & Scott 1981; Wilson & Hendrickson 1981; O'Hara *et al.* 1983; see Peters *et al.* (1976) for a review of these structure–function correlations). Although the evidence for this assumption is sparse and indirect, it stands as a likely possibility. Also, Famiglietti (1970) in the cat and Lieberman (1973) in the rat have shown that some f. terminals in the lateral geniculate nucleus are presynaptic dendrites. Our data do not address these points, but do show that f. terminals make a large contribution to the synaptic inputs of all four neurons, particularly near the retinal inputs. Presumably these spatial relationships have some as yet undetermined role in the regulation of retinogeniculate transmission (Singer 1978; Burke & Cole 1978).

R.s.d. terminals

Whereas retinal terminals are the predominant excitatory input near the soma (if f. terminals are presumed to be inhibitory), r.s.d. terminals rapidly become the predominant synaptic type only a few tens of micrometres beyond the retinal terminals and dominate on the intermediate and distal dendrites. Light microscopic observations suggest a massive input to the lateral geniculate nucleus from the

visual cortex (Guillery 1967; Hollander 1972; Gilbert & Kelly 1975; Updyke 1975; Robson 1983). Following visual cortical lesions, many r.s.d. terminals degenerate in the lateral geniculate nucleus (Jones & Powell 1969; Szentágothai *et al.* 1966; Pasik *et al.* 1973; Winfield *et al.* 1975), and this indicates that many or most of the r.s.d. terminals arise from corticogeniculate axons. However, intrageniculate collaterals of geniculocortical axons may also show degeneration from cortical lesions. Present data (Guillery 1967; Friedlander *et al.* 1981; Stanford *et al.* 1983) indicate that these collaterals probably constitute a small proportion of the degenerating axons that are observed, but without more definite data, their relative number remains unknown. Nevertheless, our tentative assumption is that most r.s.d. terminals in the lateral geniculate nucleus arise from corticogeniculate axons. Because each of our sampled neurons was a relay cell and had many hundreds of r.s.d. terminals, it seems clear that corticogeniculate axons terminate onto relay cells (Robson 1983) and not just onto interneurons (Dubin & Cleland 1977).

The great density of r.s.d. terminals at an intermediate distance from the soma indicates that these synapses could make more than just a small modulatory contribution in influencing the action potentials of the neurons, but investigators have reported little trans-synaptic excitation of relay cells following electrical stimulation of visual cortex or optic radiation (however, see Ahlsén *et al.* (1982), and for a review see Singer (1978)). However, one of the requirements for the r.s.d. terminals to function fully might be a synchronous firing pattern. Synchrony is much more likely to occur from r.l.p. synapses, because each geniculate cell receives its main excitatory retinal input from only one or a few ganglion cells (Cleland *et al.* 1971). It is possible that many of the r.s.d. synapses might be from axons of different cortical neurons (Robson 1983), and the stimulus conditions may have to be quite strict for the cortical ensemble to maximally influence the geniculate cell. Furthermore, many experiments designed to examine corticogeniculate effects (cooling cortex, etc.) have observed that the cortical influences are complex but weak (Geisert *et al.* 1981; Marrocco *et al.* 1982; for previous work see reviews by Burke & Cole (1978) and Singer (1978)). Certainly, cable theory of dendritic function (Rall 1977) suggests a significant role in synaptic transmission for these r.s.d. terminals, given their positions and densities on the dendrities. Because most of the effects so far seen are not nearly as strong as expected from this data, it seems likely that strict stimulus conditions are necessary to influence strongly the cells (for example, Schmielau & Singer 1977; Tsumoto *et al.* 1978). Conversely, the postsynaptic potentials produced by these profiles might be smaller than those from the retinal terminals, resulting in little or no direct action potentials generated from the neuron, but modulating the level of excitation for other inputs.

Total synaptic inputs

Our estimates for neurons X2 and Y2 indicate that they received a total of about 4000–5000 synaptic contacts on their dendritic arbors with the greatest number and density of synapses occurring at 50–100 μm away from the soma. Because neuron Y2 has a hemispherical arrangement of its dendrites rather than the more typical sphere seen for Y-cells, the synaptic counts might represent only about one-half of that for cell Y1. A Sholl ring analysis (Sholl 1955; see table 1 footnote)

also indicates this may be the case because the total dendritic intersections for cell Y1 was 142 and only 74 for cell Y2. However, a previous Sholl ring analysis of Y-cells (Friedlander *et al.* 1981) places a value of 142 near the upper limit for Y-cells, whereas 74 falls nearer the middle of the range for both X- and Y-cells (X1 had 63 dendritic intersections). Therefore, our synaptic counts for cells X2 and Y2 may be representative of average neurons in the lateral geniculate nucleus. If so, then many geniculate neurons receive about 300–600 r.l.p. synapses, about 1900–2600 r.s.d. synapses, and about 1800–2000 f. synapses. More neurons will have to be analysed to determine how reliable these estimates prove to be. To summarize these results in a graphic manner, the diagram of figure 16 shows the synaptic relations for an X-cell and a Y-cell including the *relative* number and distribution of the synaptic types.

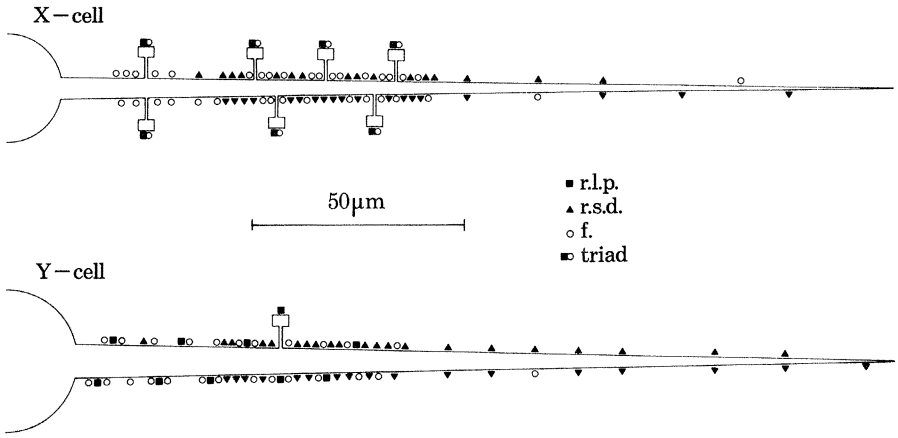

FIGURE 16. Diagrammatic representation of the distribution of synaptic terminals onto a dendrite of an X- and Y-cell, respectively. Only a single dendrite for each cell type is schematized owing to size and space limitations. Each type of synaptic terminal (r.l.p., r.s.d. f.) is represented by a different symbol. Triadic arrangements are also shown with a separate symbol. The density (synapses per micrometre of dendritic length) of each synaptic terminal type is also represented in the figure by the relative number of synapses along the dendrite. Dendritic appendages are denoted by the T-shaped attachments to the dendrites. Although all of the small squares represent f. terminals, many or most of these may be further divided into f. 1 and f. 2 types. A quantitative judgement was not made for each f. type, and they are therefore shown as equal for both the X- and Y-cell. However, the triadic arrangements always involved clear f. 2 type terminals and were very prominent for the X-cells. Also, there appeared to be a predominance of f. 1 type terminals onto the Y-cells. As presented in this diagram, the X-cell differs from the Y-cell in having many triadic arrangements involving retinal inputs and f. 2 type terminals. When present on a Y-cell, dendritic appendages are contacted by retinal terminals, but there are almost no triadic arrangements formed. Also the Y-cell has more r.l.p. terminals closer to the soma than does the X-cell.

Relay cell collaterals

Many geniculate relay neurons send collaterals into the perigeniculate nucleus as their axons ascend to the visual cortex (Jones 1975; Ferster & LeVay 1978; Ahlsén *et al.* 1978; Friedlander *et al.* 1981; Stanford *et al.* 1983). Some also have collaterals within the lateral geniculate nucleus (Friedlander *et al.* 1981; Stanford *et al.* 1983). Our fine structural examination of the morphology of a single sample of each type of collateral indicate that these terminals contain round vesicles and make

asymmetrical synapses. They are similar to geniculocortical terminals (LeVay 1973; LeVay & Gilbert 1976) and to corticogeniculate r.s.d. terminals (Jones & Powell 1969; Pasik *et al.* 1973; Winfield *et al.* 1979). Although some relay cell collaterals could be mistaken for corticogeniculate r.s.d. terminals, Ide (1982) described similar terminals in the perigeniculate nucleus and suggested that they have enough characteristics that are different from r.s.d. terminals to distinguish them as a separate terminal type. She calls these r.l.d. terminals.

The significance of the intrageniculate collaterals is uncertain because the dendritic position and type of cell these terminals contact is not known. Their relative sparseness, particularly from Y-cells (Friedlander *et al.* 1981), suggests a lesser influence in geniculate processing compared to other sources. None the less, these collaterals do exist and should not be functionally dismissed. By using similar reasoning, the position of geniculate relay cell collateral terminals onto the very proximal dendrites of cells in the perigeniculate nucleus indicates that they constitute a functionally important source of input to these cells. Electrophysiological data also demonstrate that geniculate relay cells greatly influence the cells of the perigeniculate nucleus (Dubin & Cleland 1977; Alhsén & Lindström 1982). Additionally, perigeniculate cells send their own axons back into the laminae of the lateral geniculate nucleus (Ahlsén & Lindström 1978). In the rat these axons end as f. 1 terminals (O'Hara *et al.* 1980; Montero & Scott 1981). Therefore, the perigeniculate nucleus seems to be involved in an inhibitory feedback loop, and this loop is capable of being influenced from the cortex and brainstem (see Singer (1978) and Burke & Cole (1978) for reviews). Owing to the abundant number of f. 1 synapses made onto Y-cells, as opposed to the triadic arrangements using f. 2 synapses for X-cells, this perigeniculate nucleus loop may play a more significant role for visual processing in the Y-cell than in the X-cell pathway. In any case, it is not at all clear what function the perigeniculate loop provides, although several suggestions have been published (for example, Singer 1978; Dubin & Cleland 1977; So & Shapley 1981; Schmielau 1979), and we also cannot be sure that the f. 1 terminals we have seen in the cat are actually from the axons of perigeniculate neurons.

Dendritic appendages

For both X- and Y-cells, every dendritic appendage had associated with it an r.l.p. and usually an f. terminal. Furthermore, appendages were the main points of r.l.p. contacts for the two X-cells of this sample, whereas the Y-cells had most of their r.l.p. contacts onto proximal dendrites and along secondary dendrites near the primary branch points. This suggests that, in X-cells, dendritic appendages should play a significant role in the processing of retinal signals. The function of dendritic appendages (usually called 'spines' in many cases) is not known, although several theories have been published (Chang 1952; Diamond *et al.* 1970; Peters & Kaiserman-Abramov 1970; Swindale 1981; Crick 1982; Koch & Poggio 1983). Many of these authors have pointed out that the small neck of the appendages is likely to produce an increase in the resistance along the electrotonic route to the soma, resulting in a reduction in the effectiveness of a retinal action potential at the soma or initial segment. The total effect might then be a reduction in the transfer function between the optic tract axons and geniculate neurons; that is, the action potentials produced in the geniculate neuron from its retinal input(s)

would be less than if the r.l.p. synapses occurred directly onto the main dendrites. Consistent with this are the observations that geniculate X-cells, which typically have many dendritic appendages, exhibit much less spontaneous activity than do their retinal afferents, whereas Y-cells typically have few appendages and exhibit nearly the same activity as their retinal inputs (Bullier & Norton 1979; Fukuda & Stone 1976). Although Friedlander *et al.* (1981) have described some Y-cells with numerous appendages, we have not yet studied one at the electron microscopic level. From the above discussion, it is possible that spiny Y-cells might have a reduced transfer function.

Triadic arrangements

The serial reconstructions of short lengths of dendrites for cells X2 and Y2 demonstrated that, along with the dendritic appendages, there were many triads related to retinal inputs for the X-cell, but very few such arrangements for the Y-cell. The data are consistent with the observations of Rapisardi & Miles (1984) that dendrites with many appendages have more triads than do dendrites with few or no such appendages. Additionally, the f. terminals associated with triads (for either X- or Y-cells) were of the f. 2 type, whereas most f. terminals not associated with triads were morphologically different (and typically of the f. 1 type). This difference in synaptic morphology suggests that at least these two f. types probably represent different classes rather than ends of a continuum. The association of triads with X-cells means that these cells are greatly influenced by a presumptive inhibitory population of terminals that is not predominant on Y-cells. Conversely, f. 1 terminals probably influence Y-cells more than X-cells. Thus, visual information appears to be modified by specific morphological substrates which differ between X- and Y-cells. The source of these different f. terminals remains an important question for future study.

As with dendritic appendages, the functional significance of the triads in the lateral geniculate nucleus is unknown. They are most likely to be related to inhibition involving the retinal afferent signals (for example, Lieberman & Webster 1972; Pasik *et al.* 1976; Stevens & Gerstein 1976). Differential inhibitory influences have been observed for X- versus Y-cells (Fukuda & Stone 1976; Singer & Bedworth 1976), but triadic arrangements would not seem to be necessary to mediate such inhibition; that is, no retina-to-f. synapses are required. Bullier & Norton (1979) have suggested that signals from the retina along the X-cell pathway to cortex are modified by the triadic arrangements, whereas the signals along the Y-cell pathway are basically unaffected. Rapisardi & Miles (1984) have suggested that triads mediate a feed-forward inhibition which causes the X-cells of the lateral geniculate nucleus to be less transient in their response than their retinal X-cell inputs. The reason for any of these possibilities is still obscure, but it seems clear from many studies that the X-cell system in the cat's lateral geniculate nucleus uses inhibitory mechanisms more than Y-cells and triads undoubtedly are the morphological substrate for some of these mechanisms. In this regard, one possible function of the circuitry of the lateral geniculate nucleus would be to modify incoming retinal signals of X-cells as a first step in central visual processing, whereas the Y-cell system would produce little change in this respect.

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