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MEMBRANE PROPERTIES OF MORPHOLOGICALLY IDENTIFIED X AND Y CELLS IN THE LATERAL GENICULATE NUCLEUS OF THE CAT *IN VITRO*

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SUMMARY

1. The membrane properties and the electrotonic features of cells in lamina A of the cat dorsal lateral geniculate nucleus (l.g.n.) were studied using an *in vitro* slice preparation.

2. Following intrasomatic injection of horseradish peroxidase (HRP) each neurone was classified as an X ($n = 20$) or a Y ($n = 27$) cell on the basis of its morphology. For both classes, the frequency distribution of soma area was similar to that reported *in vivo* where the identification of X and Y cells in lamina A of the cat l.g.n. was based on physiological criteria.

3. No difference was observed in the mean resting membrane potential between the two classes of cells. However, the input resistance (R_N) of X cells was greater (82 MΩ) and their membrane time constant (τ_0) longer (22 ms) than of Y cells (R_N, 32 MΩ; τ_0, 15 ms).

4. Using a simple neuronal model, the calculated electrotonic length (L) and the dendritic to somatic conductance ratio (ρ) were similar for the two classes of cells. The mean value of L (0·7) and ρ (1·9) suggests that both X and Y cells are electrically compact.

5. The specific membrane resistance (R_m, 28000 Ω cm^2) of X cells, calculated using two different approaches, was found to be higher than that of Y cells (17000 Ω cm^2).

6. The implication of these results for the integration of synaptic signals in the two classes of l.g.n. cells and the feasibility of differentiating between X and Y cells on the basis of their membrane properties are discussed.

INTRODUCTION

The dorsal lateral geniculate nucleus (l.g.n.) of the cat is a well-characterized structure both in terms of morphology and physiology (Singer, 1977; Burke & Cole,

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1978; Sherman & Spear, 1982). Cells in this nucleus are known to possess characteristic morphological features and electrophysiological properties in response to visual stimulation. Thus, in the cat, X cells when compared to Y cells tend to have more slowly conducting axons, more linear spatial summation in their receptive fields, smaller receptive field centres and more heterogeneous fields based on spatio-temporal maps (Cleland, Dubin & Levick, 1971; Shapley & Hochstein, 1975; Bullier & Norton, 1979). Morphologically different cell types have been observed in the l.g.n. (Guillery, 1966; LeVay & Ferster, 1977) and recently it has been possible to characterize the morphological differences of physiologically identified X and Y cells. They include: soma size, geometry of the dendritic tree, number and complexity of appendages and axon diameter (Friedlander, Lin, Stanford & Sherman, 1981). However, the questions of how the disparity of morphological structure between X and Y cells affect their membrane properties and how these correlate with their physiological function have not yet been addressed.

Using an *in vitro* preparation of the cat l.g.n. we have now studied the passive membrane properties and the electrotonic structure of individual l.g.n. cells, each identified as X or Y on the basis of their morphology following intrasomatic injection of horseradish peroxidase (HRP). Preliminary reports of some of these results have been published (Crunelli, Leresche & Parnavelas, 1986*a*, *b*).

METHODS

Brains from anaesthetized (2:1, O_2:N_2O, 1·2% halothane) cats (1·0–3·5 kg) were quickly dissected to a final block of tissue (2 × 1 × 1 cm) containing the l.g.n. Slices of the l.g.n. (500–600 μm thick) were cut from this block using a Vibroslice (Campden Instr.) with such an angle as to preserve the final portion of the optic tract. Slices were then transferred to a recording chamber (modified from Haas, Schaerer & Vosmansky, 1979) where they were perfused with a warmed (35 °C), oxygenated (95% O_2, 5% CO_2) medium containing (mM): NaCl, 134; KCl, 5; KH_2PO_4, 1·25; $MgSO_4$, 2; $CaCl_2$, 2; $NaHCO_3$, 16; and glucose, 10 (Crunelli, Forda & Kelly, 1983). Intracellular glass micro-electrodes (GC 120TF Clark Electr. Instr.) were filled with a solution of 4–6% HRP in 0·5 M-Tris chloride or 0·5 M-potassium acetate and used only if their resistance was less than 50 MΩ and their time to peak (in response to a square-wave current pulse) was shorter than 0·2 ms. Voltage signals were recorded with an electrometer (WP Instr., mod 707) and stored on a RACAL FM 4D tape-recorder for later analysis (Crunelli, Forda, Kelly & Wise, 1983).

For a meaningful application of the neurone model (Rall, 1977) used to calculate electrotonic length (L) and dendritic to somatic conductance ratio (ρ) the following assumptions were considered (cf. Brown, Perkel, Norris & Peacock, 1981*b*; Crunelli, Kelly, Leresche & Pirchio, 1987*a*): (a) that at each dendritic bifurcation point the 3/2 power rule is satisfied (Bloomfield & Sherman, 1984); (b) that all dendrites terminate at the same distance from the soma (cf. Rall, 1977; Stafstrom, Schwindt & Crill, 1984); (c) that the membrane behaves ohmically in the voltage region where L and ρ are measured (Fig. 5) and (d) that synaptic contamination is not present. In those cells where spontaneous synaptic potentials were observed, application of tetrodotoxin (10^{-6} M) did not produce any change in the values of L and ρ (cf. Stafstrom *et al.* 1984). All the voltage records used for the analysis were always collected before injecting HRP into the cell and it is highly unlikely that during this period sufficient HRP could have leaked out of the electrode because of its molecular weight and viscosity (cf. Brown & Fyffe, 1984). Indeed in a few cells where measurements were taken after a 10–15 min period of HRP injection, the passive membrane properties were similar to those obtained in the same cells before the injection. The similarity in the results obtained using electrodes with and without HRP again stressed the lack of any major problem associated with the use of this substance (Table 1).

The computer analysis and the two methods (Johnston, 1981; Brown *et al.* 1981*b*) used to calculate L and ρ were identical to those previously described from this laboratory (Crunelli *et al.*

1987*a*). In eleven out of the forty-seven morphologically classified neurones, the electrotonic parameters could not be calculated since it was impossible to extract the first equalizing time constant even from the averaged ($n = 15$) signal due to the poor quality of the voltage recordings. Moreover, the method of Johnston (1981) could be applied for mathematical reasons only to thirty-two cells and it gave, on average, slightly bigger values of L and ρ than the method of Brown *et al.* (1981*b*) (cf. Brown, Fricke & Perkel, 1981*a*; Brown *et al.* 1981*b*; Crunelli *et al.* 1987*a*). The specific membrane resistance (R_m) was calculated from the equation

$$R_m = \tau_0 / C_m, \tag{1}$$

where τ_0 is the membrane time constant of the cell and C_m is the specific membrane capacitance, or using the equation (Rall, 1977)

$$R_m = R_N A_T \frac{\tanh L}{L}, \tag{2}$$

where R_N is the membrane input resistance, A_T is the total surface area (soma + dendrites) and L is the electrotonic length.

The protocol used for intrasomatic injection of HRP was similar to the one described previously (Crunelli *et al.* 1987*a*). Following successful impalement and injection of HRP in an individual neurone, the micro-electrode was withdrawn and a new penetration was made at least 500 μm away. No more than two cells were injected per slice. At least 45 min after the last cell had been injected, the slice was placed in a fixative containing 1% paraformaldehyde, 1·25% glutaraldehyde in 0·12 M-phosphate buffer (pH 7·2–7·4) for 2 h. It was subsequently transferred into 0·1 M-phosphate buffer and on the following day embedded in 4% agar, cut at 60 μm with a Vibroslice and reacted with 3,3′-diaminobenzidine and H_2O_2. Sections through most slices were then mounted on slides and examined with the light microscope. However, a number of sections containing representative X or Y cells were osmicated (1% OsO_4 for $\frac{1}{2}$ h), stained with aqueous 1% uranyl acetate for $\frac{1}{2}$ h, dehydrated through a graded ethanol series and embedded in Araldite. Ultra-thin sections were then cut and examined with the electron microscope.

The classification of recovered cells into X or Y was performed by one of us blind to the electrophysiological results, and based on the morphological features of physiologically identified X and Y cells of the cat l.g.n. *in vivo*. When compared to Y cells (cf. Fig. 30 of Friedlander *et al.* 1981) X cells possess: (a) a smaller cell body, (b) dendrites which are not orientated radially around the soma, (c) dendrites of smaller diameter, (d) more numerous and complex appendages, (e) a dendritic tree that is usually contained in the same lamina as the cell body and (f) at times, a cytoplasmic laminated body when subjected to electron microscopic analysis (Morales, Duncan & Rehmet, 1964; LeVay & Ferster, 1977; Schmidt & Hirsch, 1980). The area of a spheroid was used to approximate the surface area of each soma and the surface area of dendrites was estimated by measuring dendritic diameters under 100× objective and dendritic lengths, from camera lucida drawings, with the aid of a computer (Bioquant, R. & M. Biometrics Inc.). It should be mentioned that there are errors associated with such morphological measurements. Shrinkage of the tissue, calculated by measuring the thickness of lamina A in a slice before and after fixation and tissue processing, was estimated to be 25–30%. In addition, lack of a complete three-dimensional reconstruction and inability to accurately measure the areas of all fine dendritic appendages contribute to over-all lower values of neuronal surface areas.

RESULTS

The findings presented here are based on stable intracellular recordings obtained with HRP-filled electrodes from fifty-nine cells located in lamina A of the cat l.g.n. The individual laminae of the l.g.n. were easily recognized in the tissue slices and examination with the light and electron microscope showed the neuronal and synaptic morphology to be very well preserved in slices for at least a few hours (Crunelli, Leresche, Hynd, Patel & Parnavelas, 1987*b*). Physiologically, resting membrane potentials were stable, action potentials had clear overshoots and synaptic potentials were present following electrical stimulation of the optic tract.

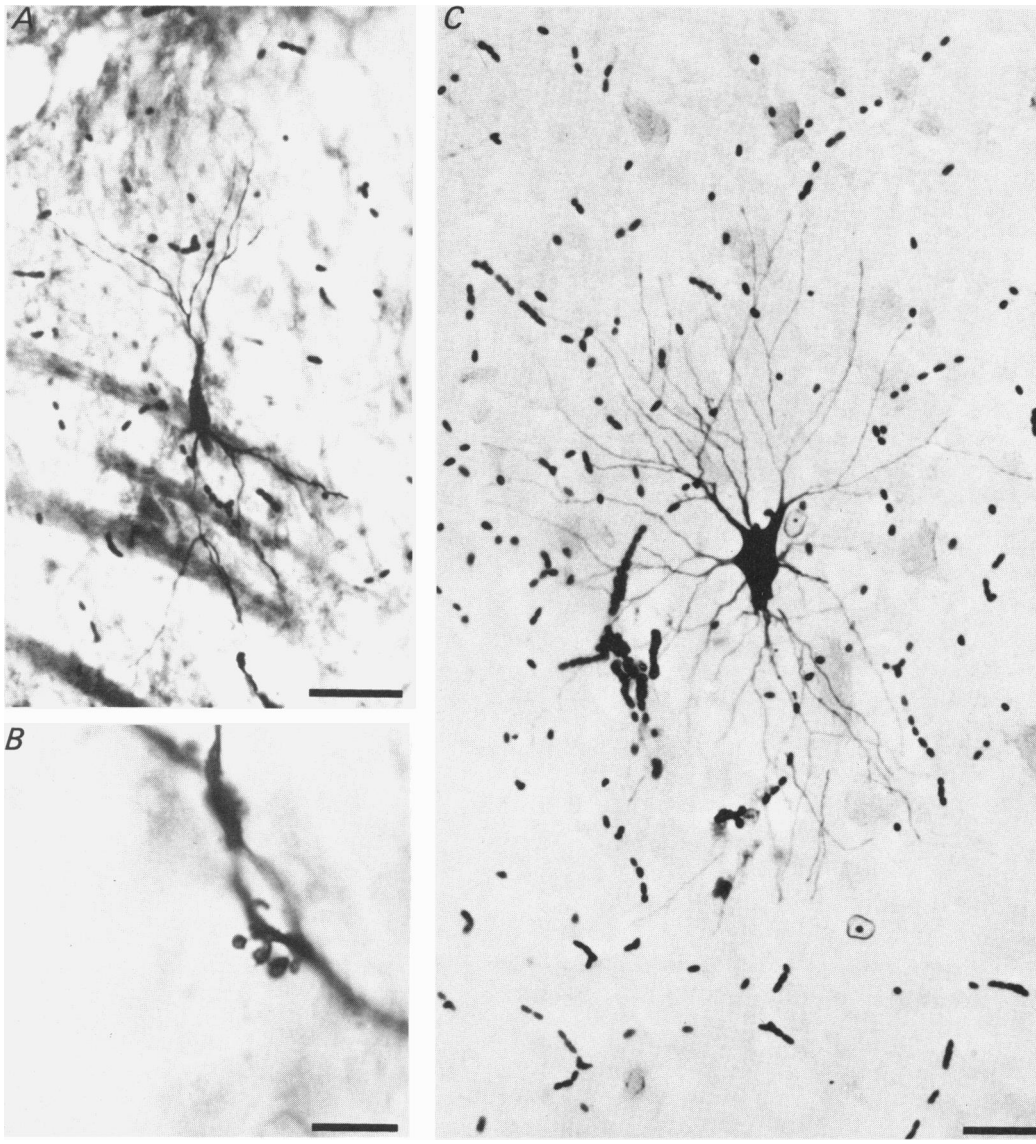

Fig. 1. *A*, photomicrograph of an HRP-injected cell from a 60 μm thick section through lamina A. Its morphological features are typical of X cells. Its rather elongated dendritic field is orthogonal to the lamination. This section was prepared for electron microscopy. *B*, a dendrite of the X cell shown in *A* giving rise to a cluster of appendages. *C*, photomicrograph of another HRP-injected cell with radially orientated dendrites classified morphologically as a Y cell. See text for further details. Calibration bar equals 50 μm for *A* and *C*, and 15 μm for *B*.

Morphological analysis

Fifty-six cells were recovered out of the fifty-nine cells injected with HRP (95%). One of the lost cells, probably a glial cell, had a high resting potential (−80 mV) and showed no action or synaptic potentials following direct current injection or electrical stimulation of the optic tract. Of the fifty-six neurones recovered, only forty-seven were filled sufficiently to allow their anatomical classification. This was performed by one of us who had no previous knowledge of the electrophysiological results. Using the already published morphological features of X and Y cells *in vivo* (cf. Methods and Friedlander *et al.* 1981), twenty cells were classified as X and twenty-seven as Y

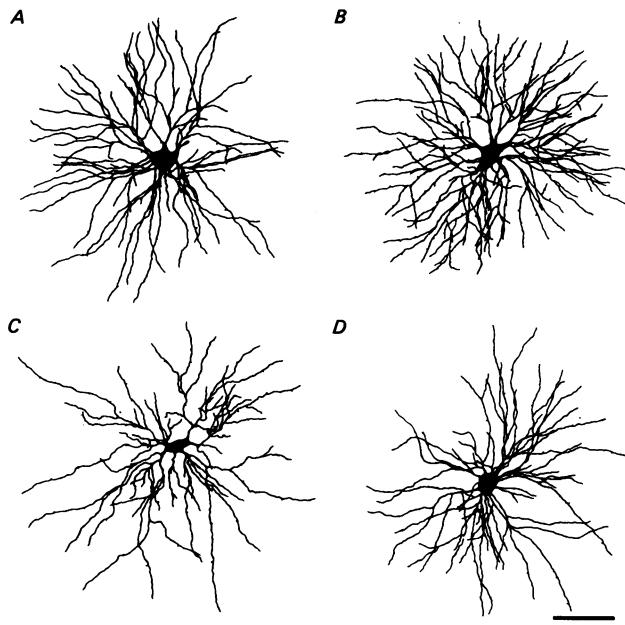

Fig. 2. Camera lucida reconstruction of four typical HRP-injected Y cells in lamina A of the cat l.g.n. Their perikaria vary considerably in shape and size but their dendrites, which are orientated radially, are relatively free of appendages. Calibration bar equals 100 μm.

(Figs. 1–3). The two neurones shown in Fig. 1 clearly show the distinctive morphological features of X and Y l.g.n. cells encountered in our sample. Thus the neurone shown in Fig. 1*A* had a small soma (cross-sectional area, 230 μm^2), a total surface area of 27000 μm^2 and was classified as an X cell. Its dendrites were asymmetrically elongated in a plane orthogonal to the lamination and possessed numerous and complex, grape-like appendages particularly near branch points close to the soma (Fig. 1*B*). The neurone shown in Fig. 1*C* was classified as a Y cell: its soma was much larger (690 μm^2) and its total surface area measured 83000 μm^2. The dendrites of this cell were symmetrically distributed around the cell body and possessed rather few single appendages.

The mean cross-sectional area of the soma (A_S) of all X cells was 264 ± 13 μm^2

(±S.E. of mean) and significantly different from that of the Y cells (473±21 μm^2). These values are similar to those obtained for physiologically identified X and Y cells *in vivo* by Friedlander *et al.* (1981) (X cells, 219 μm^2; Y cells, 493 μm^2). The frequency distribution of A_S was also similar to the one found *in vivo* and showed our sample to contain fewer X cells with A_S smaller than 100 μm^2 (Fig. 4*A*). The total surface area (soma+dendrites) (A_T) was calculated only for those cells which appeared stained in their entirety. While ten Y cells easily satisfied this additional condition (Fig. 2), unfortunately only four X cells were considered acceptable for such an

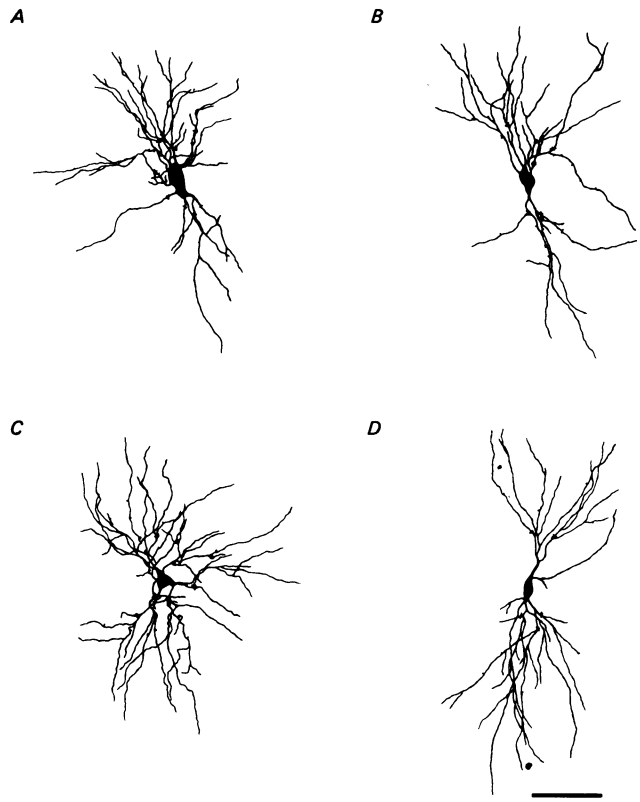

Fig. 3. Camera lucida reconstruction of four typical HRP-injected X cells in lamina A of the cat l.g.n. Their dendrites are generally elongated and give rise to clusters of appendages near branch points close to the soma. Calibration bar equals 100 μm.

analysis (Fig. 3). A significant correlation ($r = 0{\cdot}65$, $P < 0{\cdot}01$) was observed between A_S and A_T, suggesting that a larger dendritic domain was a feature of cells with bigger somata (Fig. 4*B*).

Electrophysiological analysis

There was no difference in the mean resting membrane potential between X and Y cells (Table 1). Their steady-state voltage–current relationships were also similar (Fig. 5): they showed a linear portion in the range −55 to −75 mV and marked

rectification at both hyperpolarized and depolarized levels of the membrane potential. The measurements of R_N and τ_0 were all taken from hyperpolarizing electrotonic potentials shown to lie in this linear portion of the voltage–current plot (Fig. 5). To exclude the presence of active conductances in these hyperpolarizing electrotonic potentials, voltage–current plots were also constructed at times earlier than steady-state and they too appeared to be linear up to 15–20 mV below the resting membrane potential.

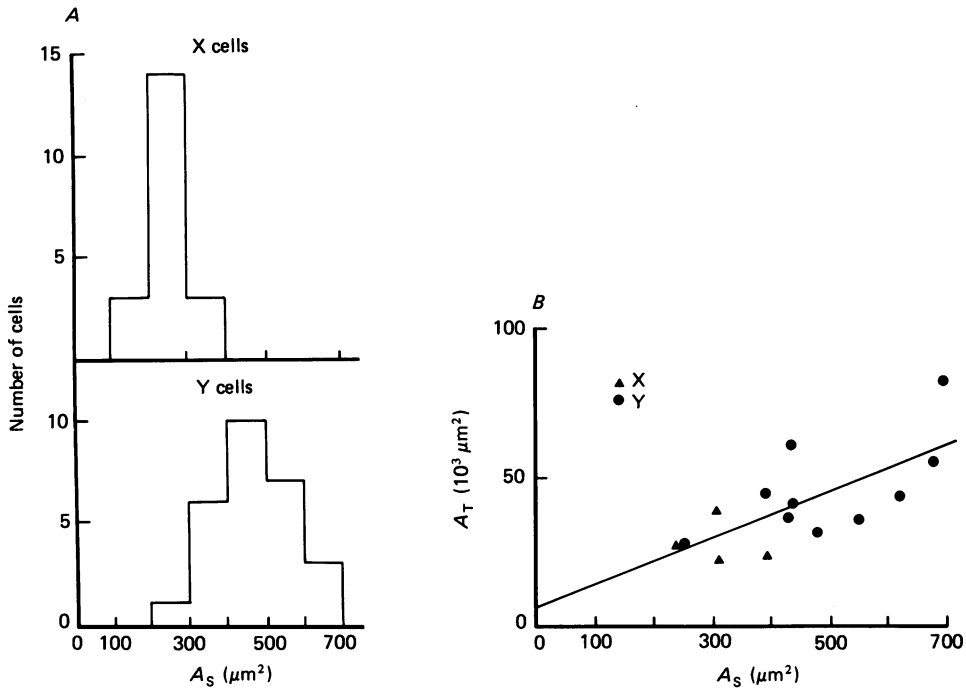

Fig. 4. *A*, frequency distribution of cross-sectional soma area (A_S) of X and Y l.g.n. cells. Note the small overlap in A_S between the two classes of cells in the range 200–400 μm^2. *B*, plot of A_S *versus* total surface area (A_T). No correlation was found for either the X or Y class of cells, but when the two classes were pooled there was a significant correlation between A_S and A_T ($r = 0{\cdot}69$, $P < 0{\cdot}01$).

The mean R_N of X cells was significantly higher than that of Y cells (Table 1) and the frequency distribution showed a clear separation between the two classes of cells with a very small overlap in the range 40–60 MΩ (Fig. 6*A*) involving only ten cells. The mean τ_0 of X cells was also higher than that of Y cells, but the difference was only of borderline statistical significance (Table 1). Thus the frequency distribution of τ_0 showed a substantial overlap (thirty-eight cells) between the two cell populations in the range 5–25 ms (Fig. 6*B*). The electrophysiological significance of the differences in R_N and τ_0 for the X and Y cell whose morphological features are shown in Fig. 1 is visible in Fig. 5. A negative correlation was observed between R_N and A_S, as well as between R_N and A_T, the former being statistically highly significant (Fig. 7*A*). A positive correlation was also found between R_N and τ_0.

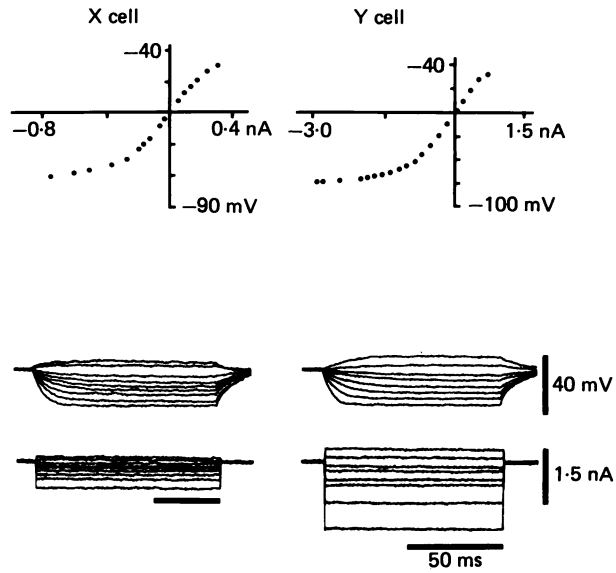

Fig. 5. Voltage–current relationship of l.g.n. cells. Voltage and current records at the bottom of the Figure show families of hyperpolarizing and depolarizing pulses of current and the corresponding voltage response (middle traces) used to construct the steady-state voltage–current relationship (plots at the top of the Figure) for the X and the Y cell shown in Fig. 1. There is a clear linear portion in both plots close to the resting potential and membrane rectification is apparent at depolarizing and particularly at hyperpolarizing potentials. Measurements of R_N and τ_0 were all performed on hyperpolarizing potentials that lay in the linear portion of the voltage–current plot. The R_N was 72 MΩ for the X and 28 MΩ for the Y cell.

TABLE 1. Passive membrane properties of cat l.g.n. relay cells

	Cells impaled with HRP electrodes				Cells impaled with potassium acetate electrodes	
	X cells		Y cells			
	Mean ± S.E.	n	Mean ± S.E.	n	Mean ± S.E.	n
V_m (mV)	−62 ± 1	20	−60 ± 2	27	−64 ± 2	12
R_N (MΩ)	82 ± 6***	20	32 ± 3	27	60 ± 7	12
τ_0 (ms)	22·4 ± 2·2*	20	14·6 ± 1·1	27	16·5 ± 1·7	12
L†	0·71 ± 0·06	13	0·82 ± 0·04	19	0·78 ± 0·07	8
ρ†	1·7 ± 0·4	13	2·1 ± 0·2	19	1·8 ± 0·4	8
H	1·29 ± 0·08	13	1·37 ± 0·06	19	1·34 ± 0·08	8
R_m^* (10^3 Ω cm²)	27·7 ± 1·9**	4	16·8 ± 2·4	10		
R_m (10^3 Ω cm²)	16·8 ± 1·2*	4	11·8 ± 1·5	10		
C_m (μF/cm²)	1·7 ± 0·2	4	1·4 ± 0·1	10		

* $P < 0·05$; ** $P < 0·01$; *** $P < 0·001$. † Results obtained using the method of Johnston (1981). R_m^*: specific membrane resistance calculated using eqn. (1) and assuming $C_m = 1$. R_m: specific membrane resistance calculated using eqn. (2).

A statistically significant difference in L and ρ was not found between the two classes of neurones and their mean values ($L = 0{\cdot}7$; $\rho = 1{\cdot}9$) indicated that both X and Y cells are electrically compact (Table 1). By calculating the attenuation factor ($H = \cosh L$) (Jack, Noble & Tsien, 1975) (Table 1) it could be shown that at the tip of the equivalent dendritic cylinder the amplitude of a voltage signal applied to the soma would be decreased by a maximum of 20–25%. No statistically significant correlation was found between L, ρ, τ_0 and R_N. The possibility that a uniform cylinder of identical regions without a soma would represent a more satisfactory model of cat l.g.n. cells

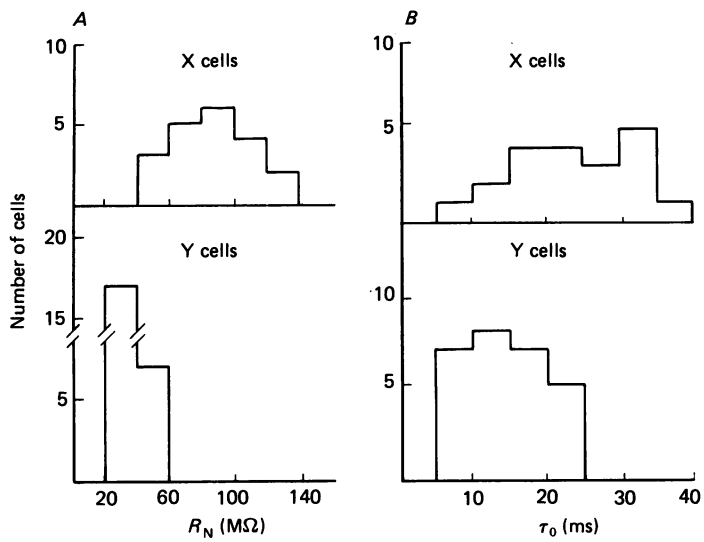

Fig. 6. Frequency distribution of input resistances (R_N, *A*) and membrane time constants (τ_0, *B*) of X and Y l.g.n. cells. Note the small overlap in R_N between the two cell classes in the range 40–60 MΩ (see Table 1 for further details).

was tested by checking whether the values 2 (τ_1/τ_0) were equal to (C_1/C_0) (coefficients associated with the time constants; Rall, 1977) (cf. Sato & Tsukahara, 1976; Brown *et al.* 1981*b*). However, for the majority of neurones the values 2 (τ_1/τ_0) were higher than (C_1/C_0), as it would occur if an isopotential region similar to the soma surrounded the point of current injection.

Throughout a variety of biological tissues of simple geometry the value of C_m has been shown to be equal or close to 1 μF/cm^2 (Cole, 1968; Jack *et al.* 1975; Brown *et al.* 1981*b*). Substituting this value in eqn. (1) and using the electrophysiologically derived values for τ_0, we have found that the R_m for X cells was higher than that for Y cells (Table 1). Using another equation, eqn. (2), R_m was calculated by combining both morphologically and electrophysiologically derived parameters. The values of R_m calculated in this way were lower (29–38%) than those obtained using eqn. (1) (Fig. 7*B*), but the R_m of X cells was still higher than of Y cells (Table 1). When the values of R_m obtained with eqn. (2) were substituted in eqn. (1), the mean value for

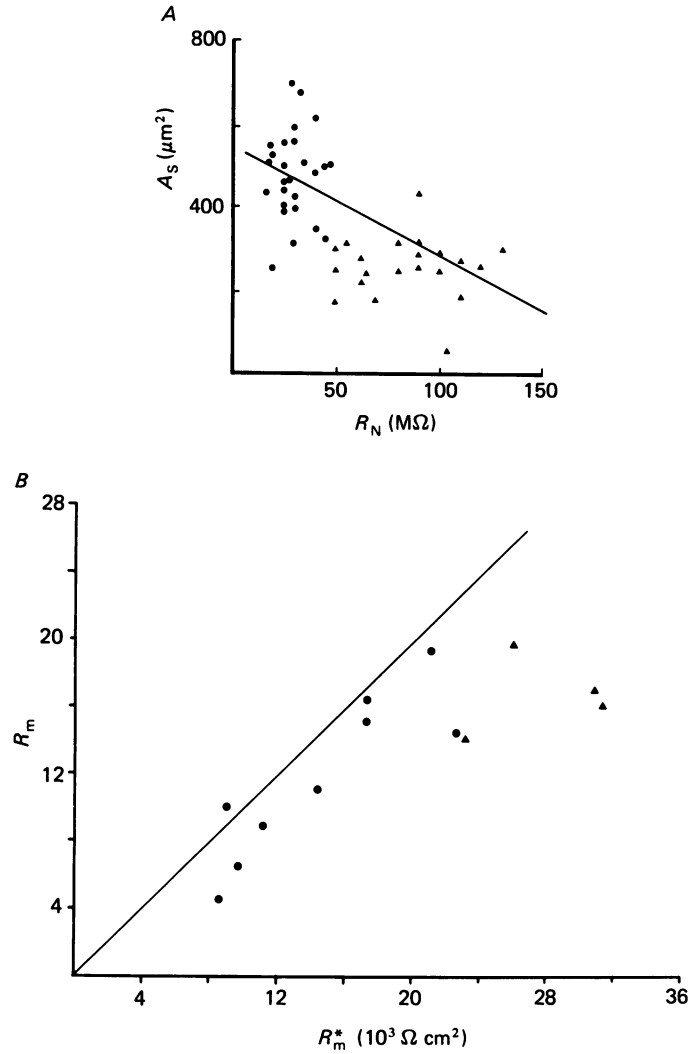

Fig. 7. *A*, plot of input resistance (R_N) *versus* cross-sectional soma area (A_S). No correlation was found for either X (▲) or Y (●) cells, but when the two classes of cells were pooled there was a high negative correlation ($r = -0{\cdot}62$; $P < 0{\cdot}001$) between R_N and A_S, indicating a higher input resistance for cells with smaller somas. *B*, plot of R_m (specific membrane resistance calculated using eqn. (2) and the anatomical measurements) *versus* R^*_m (specific membrane resistance calculated using eqn. (1) and assuming $C_m = 1$) for X (▲) and Y (●) l.g.n. cells.

C_m was 1·5 (±0·1; S.E. of mean) and there was no difference between X and Y cells (Table 1).

During the course of this study we also impaled twelve l.g.n. cells using microelectrodes containing a solution of 1 M-potassium acetate. The results obtained from these neurones showed mean values of L and ρ identical to those from the forty-seven

cells injected with HRP (Table 1). Their R_N and τ_0 values were also similar to those obtained by combining the results from both classes of morphologically identified neurones. Although in this study we did not look systematically at the active membrane properties of cat l.g.n. cells, it is worth mentioning that no major differences were observed between the action potentials of X and Y cells and that low-threshold, Ca^{2+}-dependent potentials, recently described as a property of principal neurones of the rat l.g.n. (Hirsch, Burnod & Korn, 1985; Crunelli *et al.* 1987*a*) and other thalamic nuclei of guinea-pig and cat (Deschenes, Paradis, Roy & Steriade, 1984; Jahnsen & Llinás, 1984*a*), were present in all but one (histologically unrecovered) of the impaled neurones.

DISCUSSION

The main conclusion of this investigation is that in the cat l.g.n. the R_N of X cells is higher, the τ_0 longer and the R_m greater than that of Y cells and that neurones of both classes are electrically compact.

Classification of impaled cells

Using Golgi impregnation techniques, Guillery (1966) described three distinct morphological classes of cells in lamina A of the cat l.g.n. LeVay & Ferster (1977), on the basis of indirect evidence, suggested that these classes represented X cells, Y cells and interneurones. More recently Friedlander *et al.* (1981), using intracellular injection of HRP into physiologically identified X and Y cells, have provided direct evidence showing that X and Y cells possess different morphological features. These morphological criteria have been used here to classify HRP-injected neurones as X or Y cells. The morphological identification of Y cells did not present any major difficulty, since the majority of Y cells appear to possess a striking uniformity of morphological features (Friedlander *et al.* 1981). The identification of X cells was somewhat more complicated, since physiologically identified X cells have been shown to possess a dendritic morphology similar to that of class 2 and 3 cells of Guillery (1966), the latter being the presumed l.g.n. interneurones (Friedlander *et al.* 1981). However, each of our morphologically classified X cells possessed low-threshold Ca^{2+} potentials that are said to be a feature of all thalamic relay cells in a variety of animal species (Jahnsen & Llinás, 1984*a*; Deschenes *et al.* 1984; Crunelli *et al.* 1987*a*) but absent from physiologically identified thalamic interneurones (Deschenes *et al.* 1984).

In terms of soma size, our neuronal sample appears to be fairly representative of cat l.g.n. cells in lamina A, although it contains fewer X cells with A_S smaller than 100 μm^2 (cf. Friedlander *et al.* 1981; LeVay & Ferster, 1977), probably as a result of using micro-electrodes with a different tip size. It is unlikely, however, that this has biased strongly our data. Thus, for instance, the negative correlation present between R_N and A_S suggests that the lower number of X cells with the smaller A_S probably led to an underestimation of the R_N of this cell class, due to poor impalement of the smaller neurones.

Membrane properties of l.g.n. cells

The results presented here indicate that the R_N of X cells is higher and the τ_0 longer than that of Y cells, and that both L and ρ for the two classes of cells are similar. The differences between R_N and τ_0 for the two classes of cells appear not to be a consequence of the *in vitro* technique since similar differences have recently been observed in physiologically identified X and Y cells of the cat *in vivo* (Bloomfield, Hamos & Sherman, 1985). However, *in vitro* the absolute values of R_N and τ_0 are larger than those found *in vivo*. This may be explained by both the lack of strong synaptic inputs *in vitro* and the better mechanical stability obtained during *in vitro* recordings. A small overlap is present in the frequency distribution of R_N for X and Y cells and, interestingly, a similar overlap is also present in the frequency distribution of their A_S.

The values of L and ρ for cat l.g.n. cells are lower than those of spinal motoneurones and other cells studied *in vivo* but similar to those of other neurones recorded *in vitro* (references in Brown *et al.* 1981*a*, *b*; Crunelli *et al.* 1987*a*). It is possible that the values of L and ρ obtained *in vivo* are more heavily contaminated by the presence of synaptic inputs. On the other hand, the possibility that the slicing procedure might have severed some of the most distal dendrites cannot be excluded. However, this problem was probably minimized by recording preferentially from neurones located in the middle of the slice and the calculated values of L and ρ are indeed comparable to those recently reported for l.g.n. cells *in vivo* (Bloomfield *et al.* 1985).

In agreement with the results obtained *in vivo* from physiologically identified X and Y cells (Bloomfield *et al.* 1985), we too have found, using two independent approaches, that the R_m of the former cell class is significantly larger than that of the latter one. The lower values of R_m calculated with eqn. (2) by using electrophysiologically and morphologically derived parameters must be viewed with caution because of the errors associated with the morphological measurements. Nevertheless, the difference in R_m between X and Y cells was still present and the range of C_m values (0·9–2·1) was not dissimilar to those reported for neurones with a much simpler morphology (Cole, 1968; Jack *et al.* 1975; Brown *et al.* 1981*b*).

What are the physiological consequences of our results? From the higher R_N and longer τ_0 of X cells it follows that both the spatial and the temporal summation of synaptic signals will probably be greater in X than Y cells. The values of L and ρ clearly indicate that despite their extensive dendritic arborization X and Y l.g.n. cells are electrotonically compact, i.e. that in the steady state there will be only a small decrease in the amplitude of synaptic potentials propagating passively from the dendrites to the soma. Thus retinal and cortical inputs, which tend to make synaptic contacts on proximal and distal dendrites respectively (Sherman & Spear, 1982), may have a similar efficacy at the level of the soma. Thus, contrary to the 'classical' view on the ineffectiveness of the more remote synapses (Eccles, 1964), it appears that distally generated inputs (e.g. cortical and ascending reticular pathways) will contribute substantially to the over-all output signal of l.g.n. cells. This strongly supports the idea that the l.g.n. plays a powerful gating role on the visual information travelling from the retina to the cortex and does not act as a simple relay station (Sherman & Koch, 1986). The electrical compactness does not necessarily

imply a lack of dynamic interactions between dendritically generated synaptic events. As shown for other central neurones possessing an electrotonic compactness similar to l.g.n. neurones (Traub & Llinás, 1979), the presence of different and asymmetrically distributed active conductances on the dendritic tree is certain to generate a variety of different electrical behaviours and to have profound consequences on the efficacy of synaptic inputs in these two classes of l.g.n. cells (Koch, 1985).

Finally, the feasibility of *in vitro* studies for the cat l.g.n., the electrical compactness of its neurones, and the different R_N values between X and Y cells will make it possible to identify *in vitro* those cells at the extreme ends of the R_N range as either X or Y without the use of staining techniques and to study the physiological and pharmacological properties of their somatic as well as synaptic currents generated on proximal dendrites.

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