

active dendritic properties. A preliminary note (PELLIONISZ & LLINÁS, 1975) has been published on the present study.

METHODS

The Purkinje cells of the model are represented by different types of dichotomous tree dendritic structures. The morphogenesis of these trees provides a variant of the 'skeleton' of branch-arborization in respect of lengths and angular deviations of branches on the 29×29 two-dimensional lattice (of $10 \mu\text{m}$ spacing). As is shown in Fig. 1 A, which demonstrates the basic neuronal elements of the circuitry model (cf. PELLIONISZ, LLINÁS & PERKEL, 1977), the Purkinje cell bodies are distributed on a staggered arrangement. The Purkinje cell dendritic trees are gradually thinned towards the distal end to provide a clarity of the positioning of trees and an impression about the density of the dendritic structure (Fig. 1 B). For illustrative reasons, three representative dendritic arbors are depicted in Fig. 1 C-E. Close to one-half of the 29×29 matrix points are marked by dots. Each dot represents one complete spiny branchlet on the tree. Variation of the branch distribution in these dendritic trees is indicated in Fig. 1. In C minimum dendritic overlapping is observed, and in D a large degree of overlapping is shown. In E dendritic trees with clear dendritic asymmetry is illustrated. These skeleton trees represent the distribution of the Purkinje cell's smooth dendrites and are considered an adequate model for the development of a connectivity circuit in which a rigid characterization of the neuronal connectivity is largely avoided.

Morphological structure of the Purkinje cells

All Purkinje cell dendritic arborizations are represented as a set of cable segments. Each segment has a uniform diameter but the different segments have different diameters (Fig. 1 F). The basic dimensions were obtained from Golgi-stained preparations (HILLMAN, 1969b) and electron micrographs (SOTELO, 1969). In establishing the diameters of the dendritic segments a crucial parameter is the exponent p in the equation for parent and daughter branches (RALL, 1962a).

$$a_1^p + a_2^p = a_0^p$$

which for the equivalent cylinder model is $3/2$. However, since preliminary measurements (J. MCLAREN, personal communication) indicate that this figure for first bifurcation of the Purkinje cell dendritic tree averages 1.75, this latter figure is used in the models presented in this paper unless otherwise noted. The total morphological structure of the cell is constructed in the following way.

Dendritic tree. (i) The length of the 'trunk' is separately set [normally $70 \mu\text{m}$ (HILLMAN, 1969a)]. (ii) The lengths of dendritic branches are determined by the morphogenesis of skeleton trees (PELLIONISZ *et al.*, 1977) (iii) The branch point diameter (initially $6.0 \mu\text{m}$) is established for the trunk. The diameters for each successive bifurcation, the a_1 and a_2 daughter branch and a_0 parent diameter, follow the equations $a_1^p + a_2^p = a_0^p$ and $a_1/a_2 = L_1/L_2$, where L_1 is the combined length of the remainder dendritic tree supported by the daughter branch with diameter a_1 , while L_2 is that for the other daughter branch.

Soma. The soma of the cell is assumed to be a sphere (with diameter normally set at $15 \mu\text{m}$).

Axon. The axon is constructed as consisting of three different structural parts, each being a uniform cylinder: (i) Initial segment of axon (normally with length of 25 and diameter of $2 \mu\text{m}$). (ii) Myelinated segments (of $200 \mu\text{m}$ length and $3 \mu\text{m}$ diameter). (iii) Axonal node of Ranvier (cylinder of $3 \mu\text{m}$ length and $2 \mu\text{m}$ diameter).

The morphological structure of such a Purkinje cell is shown in Fig. 1 F. Note that different scales apply for dendritic diameter and branch length and for the length and diameter of axonal segments.

Compartmentalization of the Purkinje cell model

Compartmentalization of the Purkinje cell model is shown in Fig. 2. As seen in A, each of the seven myelinated segments, the seven Ranvier nodes, and the axonal initial segments is considered as a separate spatial compartment. The electrical parameters utilized were $100 \Omega/\text{cm}$, for the intracellular medium, $6000 \Omega/\text{cm}^2$ and $1 \mu\text{F}/\text{cm}^2$ (DODGE & COOLEY, 1973) for the specific resistivity and capacitance of the soma, dendrites and nodes and infinite resistance, and $0.05 \mu\text{F}/\text{cm}^2$ for resistance and capacitance of the internode respectively. The spherical soma is equated to a cylinder of identical volume and is represented as a separate compartment. The dendritic branches are broken into thirds where the midsection represents a simple cylindrical compartment, while the adjoining three sections, at each branch, represent a combined spatial compartment. Thus, while the Purkinje cell model had a variety of dendritic branching patterns, it consisted, in every case, of 62 spatial compartments.

Each cylindrical compartment (e.g. axonal compartments, dendritic midsections, or the two adjoining thirds at the upper end of the top branches) is equated to an equivalent cylinder of two halves while the branching compartments have a three cylindrical equivalent (Fig. 2 B). If in the i neighbor compartments the diameters of cylindrical segments are d_i , the lengths are L_i , and the compartment receives k activated spines, then the V membrane potential in the equivalent circuit (C in Fig. 2) is determined by the following equation:

$$R_i = r_i \frac{4L_i}{d_i^2 \pi}, \quad R_{sp} = R_{spine}/k, \quad C = c \cdot \sum_{n=1}^i d_{ii} \cdot \pi \cdot L_n$$

(where r_i is the specific resistance of the internal medium c is the specific cross-membrane capacitance of the membrane and R_{spine} is the resistance represented by one spine).

Time function of membrane potential and Hodgkin & Huxley equations

The following equations apply for the membrane potential V as determined by the I_m cross-membrane current, I_L longitudinal current (inside the cylindrical segment) and the I_S synaptic current.

$$0 = C \frac{\delta V}{\delta T} + I_m + I_L + I_S \quad \text{where}$$

$$I_m = \frac{1}{R_{Na}}(V - V_{Na}) + \frac{1}{R_K}(V - V_K) + \frac{1}{R_L}(V - V_L)$$

$$I_L = \sum_{n=1}^i \frac{1}{R_n}(V - V_n) \quad \text{and} \quad I_S = \frac{1}{R_{sp}}(V - V_{sp})$$

Where V_{Na} , V_K and V_{sp} are the equilibrium potential values for the Na^+ and K^+ ions and for the synaptic depolarization (with the assumed values of 115 mV , -5 mV and