

those relating to  $\bar{g}_{Na}$  and  $\bar{g}_K$ . An example of this versatility is illustrated in Fig. 2 D-F where the excitability is increased from close to zero at the upper portion of the dendritic tree (top row) to a moderate level at the somatic compartment (middle row). The axonal nodes exhibit their usual high excitability (lower row). This individual treatment of spatial compartments was considered essential in order to study potential inhomogeneities of the excitability on the dendritic tree (so-called 'hot spots') associated with dendritic spikes (LLINÁS & NICHOLSON, 1971). The present paper aims at modeling the frog Purkinje cell in which dendritic spikes are not prominent, the dendritic compartments (unless otherwise specified) being considered non-excitable, passive cables.

#### Computational methods

The set of equations was solved numerically using a PDP-15 computer (Digital Equipment Corp.) with floating point processor and 32K 18-bit core memory, and the data monitored on a Tektronix 611 storage oscilloscope and stored via DEC-pack cartridge disc. The data later could be displayed using either the passive storage oscilloscope or the dynamic graphic-15 display, therefore enabling both the selecting and composing of static pictures or production of spatio-temporal display by computerized cinematographic methods.

The numerical integration was chosen as the classical Euler (explicit) integration form which requires suitably limited  $dx$  and  $dt$  to avoid instabilities of the computation. While the program automatically monitored the  $dV$  increment in every compartment and accordingly relaxed or restricted the time increment of the integration (within the extremes of 200 ns and 25  $\mu$ s) separately, in an asynchronous manner for every compartment, still the computation involved in the solution of Hodgkin-Huxley and cable equations makes this 62 compartment model work about  $5 \times 10^5$  times slower than the real time activity of Purkinje cells.

The traditional questions of boundary problems in a spatially limited model were handled in two different ways; the axonal end of the distal compartment could either have the option of 'open end' (connected to the isopotential extracellular fluid by short circuit) or 'sealed end', in which the next to last compartment echoed the potential of the last compartment with an identical value. While the uppermost dendritic branches were always considered sealed, the axonal ending could be set either way. The short circuited 'cut' ending of axon introduces a clearly visible distortion of action potential on the last nodes which is the reason for using a relatively long axon consisting of seven myelinated segments.

## RESULTS

The simulation of electrical activity of Purkinje cells is particularly advantageous since this cell produces three markedly different types of activation all of which have been studied in great detail. Thus, any Purkinje cell model which claims to be adequate, at least at first approximation, must satisfy the rather stringent requirement of producing appropriate potential waveforms for all of these three forms of activation. Namely, the propagation of the action potential evoked by antidromic electrical stimulation must result in a firing of the initial segment of the

axon and then the soma itself. The depolarization, however, should rapidly decrease upward on the dendritic structure (cf. LLINÁS *et al.*, 1969; FREEMAN & NICHOLSON, 1975). The orthodromic activation via parallel fiber synaptic input must be graded and must generate unitary simple action potentials. The model should also be able to generate the complex spike bursts which follow the climbing fiber activation (ECCLES *et al.*, 1966; LLINÁS *et al.*, 1969) without any parameter modification.

#### Antidromic activation

The spatio-temporal display of the membrane potential waveforms throughout the 62 compartment model in the case of antidromic activation is shown in Fig. 3. In this particular example the main trunk and all dendritic branches are passive RC cables. The specific Na and K conductance figures were chosen in order to arrive at an appropriate spike propagation speed through the axon and a proper waveform for the action potential. Thus  $\bar{g}_{Na} = 600 \Omega^{-1}/\text{cm}^2$  and  $\bar{g}_K = 100 \text{m}\Omega^{-1}/\text{cm}^2$  were assumed for the excitable Ranvier nodes and soma. A 50% increase of these values was assumed for the initial segment. With these values a 10 nA stimulus applied to the sixth Ranvier node generated the antidromic invasion seen in Fig. 3. Display of the intracellular voltage across the different segments indicates a rapid reduction of  $V_i$  with distance from the soma, as expected from the analysis of field potentials (LLINÁS *et al.*, 1969; FREEMAN & NICHOLSON, 1975).

#### Orthodromic activation by parallel fibers

The orthodromic activation of Purkinje cells following parallel fiber stimulation via surface electrodes has been carefully investigated in many different preparations (ECCLES *et al.*, 1966; LLINÁS *et al.*, 1969) and some theoretical consideration has been given to the possible impact of differences in integration of input carried by different spatial patterns of parallel fiber input (LLINÁS, 1971). Simulation of this type of Purkinje cell activity was obtained by current injections distributed over the dendritic tree via the dendritic spines. Thus, as seen in Fig. 2 B, the cylindrical spatial compartments may have different numbers of activated spines. The activated spine is represented by a  $100 \Omega^{-1}$  conductance increase allowing a synaptic current to be injected as shown in the equivalent circuit of Fig. 2 C.

Thus for orthodromic activity evoked by, let us say, a horizontal strip of activated parallel fibers, we assumed that each of the 16 uppermost branches received five continuously 'open' synapses during a 0.5 ms time interval. This case is shown in Figs. 3 B and 4. The off-line display of data provided a good opportunity to compare the results in the conventional electrophysiological manner (as two-dimensional graphs of time-function of membrane potential at one spatial location) with the simultaneous visualization of the depolarization wave throughout the den-