

FIG. 5. Numerical solution illustrating vertical integration of an orthodromic input applied to one side of the dendritic tree (vertical distribution). The amplitude and duration of the input are identical to that in Fig. 4, the only difference being the spatial distribution of the input. The schematic diagram to the left was taken at 2.5 ms from the onset of computation (arrow).

EPSP evoked at somatic level differed markedly both in amplitude and rising phase with different localization of parallel fiber input in varying distance from the soma. Accordingly the EPSP evoked at somatic

level produced a practically immediate action potential of soma and initial segment, and the spike propagated along the axon. Moreover, the initial spike of short latency was followed, slightly more than 2 ms later, by a second propagating spike. Only after this short 'burst' was a general decay of the depolarization visible throughout the model. Interestingly, the second spike was initiated almost simultaneously at the initial segment and soma, followed by outward propagation towards the dendrites and axon.

Activation of Purkinje cell by climbing fiber

The distribution of membrane potential in the case of a climbing fiber activation of the same model Purkinje cell is shown in Fig. 6 B and compared with the actual record from a frog Purkinje cell (Fig. 6 A). This highly stereotyped all-or-none spike, which is followed by several (normally 3-5 but in some cases up to 12) oscillatory wavelets, has been observed frequently in the cerebellum of the frog (LLINÁS *et al.*, 1969; FREEMAN, 1969; FABER & KORN, 1970; RUSHMER & WOODWARD, 1971; LLINÁS, PRECHT & CLARKE, 1971; HACKETT, 1972, 1976). While the climbing fiber-Purkinje cell synapse is well understood morphologically (LARRAMENDI & VICTOR, 1967; HILLMAN, 1969b) and electrophysiologically (ECCLES *et al.*, 1966; LLINÁS & NICHOLSON, 1976), the exact mechanism which generates this characteristic spike burst has remained unclear hitherto and only speculative statements are available (ECCLES *et al.*, 1966; MARTINEZ *et al.*, 1971).

Climbing fiber activation of the Purkinje cell model was simulated by activating five synapses on each

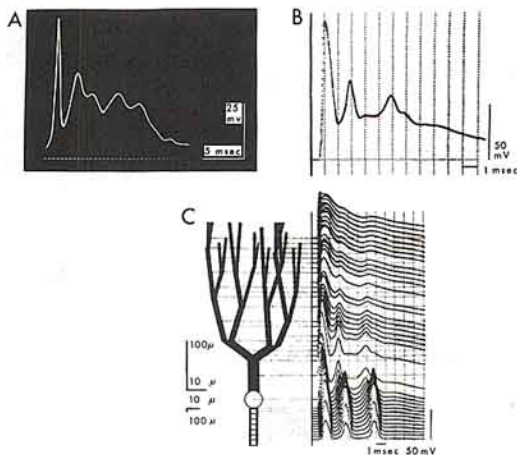


FIG. 6. Climbing fiber activation of Purkinje cell. In A, sample of actual intracellular recording of the climbing fiber evoked spike burst in a frog Purkinje cell. The first spike is followed by a highly stereotyped pattern of wavelets. B: Numerical solution illustrating action potential waveform at Purkinje cell somatic level by a synaptic input equivalent to the distribution of climbing fiber synapses. The similarities with the experimental results are evident. In C similar activation as in B illustrating membrane potential throughout the 62 compartments. For further explanation, see text.