

### Wilfrid Rall

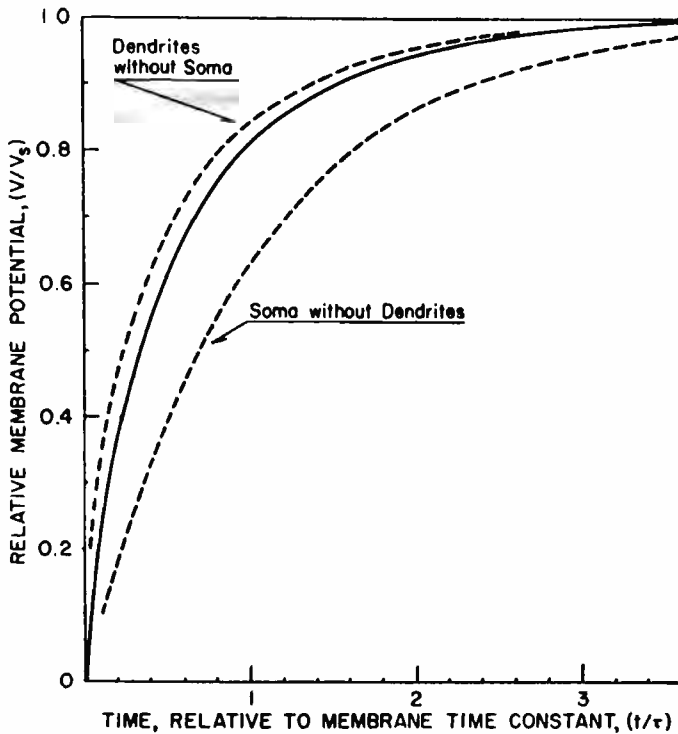
New information about motoneuron membranes has been obtained in recent experiments in which intracellular electrodes were used for both stimulation and recording at the motoneuron soma (1–6). Unexpectedly low membrane time-constant values have been inferred from the sub-threshold transients of membrane potential observed when constant current was applied across the soma membrane (2–4). It is shown in this report, however, that these experimental transients are theoretically consistent with significantly larger membrane time-constant values, provided that the cablelike properties of dendrites are taken into account. This correction removes the apparent discrepancy (3–5) between the soma membrane time constant and the time constant of synaptic potential decay and thus removes the need for special explanations, such as a hypothetical prolongation of synaptic depolarizing activity (4, 6), or a prolongation of soma synaptic potential by electrotonic spread from a larger and slower synaptic potential postulated to occur in the dendrites (5).

The membrane time constant  $\tau$  is defined as the product of passive membrane resistance and capacitance. The assumption (2–4, 6) that the experimentally observed membrane transients may be regarded as exponential curves having this time constant  $\tau$  would be valid only if constant current were applied uniformly to the entire membrane surface. For the experiments in question, this could be true only for the hypothetical case of a *soma without dendrites*. The lower dashed curve in Fig. 1 illustrates the exponential time course of membrane potential change  $V$ , relative to its final steady value  $V_s$  for this hypothetical case.

Since the motoneurons are known to possess several large dendrites, a significant portion of the current applied to the soma must spread (electrotonically) along these several dendrites. This will change the time course of soma membrane potential. For example, as the size and number of dendrites is increased relative to soma size, there is a limiting case, *dendrites without soma*. This case is illustrated by the upper dashed curve in Fig. 1, on the assumption that these dendrites have the same membrane time constant  $\tau$  and that they may be represented as cylinders of infinite length. This time course can be precisely expressed as

$$V/V_s = \operatorname{erf} \sqrt{t/\tau}$$

for the membrane potential at the point (soma) where constant current is applied across the membrane of each dendrite. It is the same as that



**Figure 1**

Membrane potential transients at the neuron soma and origins of dendrites, when constant current is applied across the soma membrane.

obtained in the more familiar problem of electrotonic potential beneath an electrode ( $x = 0$ ), when constant current is applied between external electrodes placed far apart on a cylindrical axon (7). This curve is not a simple exponential: the time required to reach half of the steady value  $V_s$  is one-third of the time required in the lower dashed curve, while the time required to reach 90 percent of  $V_s$  is about three-fifths of that required in the lower dashed curve.

The middle curve in Fig. 1 corresponds to an intermediate relation between dendrites and soma (8). It has been assumed that soma and dendrite membranes have the same membrane time constant and that the membrane potential at any moment is uniform over the soma surface (9), up to and including the origins of the dendrites. The dendrites can be treated either as cylinders of infinite length or as structures which taper and branch exponentially.

This intermediate curve was calculated with a value of 5 for the ratio between the steady-state membrane current drawn by the dendrites and

the steady-state current drawn by the soma membrane. This value is theoretically consistent with the specific example of a soma with six cylindrical dendrites (used in 1 and 6, as well as in 3), provided that a value of about 2000 ohm cm<sup>2</sup> is used for the membrane resistivity. Since this example probably underestimates the size and number of dendrites (1, p. 322), it is predicted that the time course of soma membrane potential change, when constant current is applied to the soma, will lie *between* the two upper curves in Fig. 1, for many motoneurons.

On the basis of this theoretical prediction, the membrane time constant can be estimated as being the time required for the experimental transients to reach about 82 percent of the final steady value. Since, however, the experimental error permits exponential curves to be fitted to the experimental transients (2-4), it should be noted that the time constants of such curves can be expected to be smaller than the actual membrane time constant, by a factor of about 2. It appears, therefore, that these experimental transients do not conflict significantly with the earlier estimate (10), of about 4 msec for the membrane time constant of cat motoneurons, which was based on the decay time constant of synaptic potentials (10), and of monosynaptic facilitation (11).

This is consistent with the simple notion of synaptic potential decay as a purely passive process, having the same characteristics on both soma and dendrites (12).

---

## References and Notes

1. J. S. Coombs, J. C. Eccles, P. Fatt, *J. Physiol.* **130**, 291 (1955).
2. T. Araki and T. Otani, *J. Neurophysiol.* **18**, 472 (1955).
3. K. Frank and M. G. F. Fuortes, *J. Physiol.* **134**, 451 (1956).
4. J. S. Coombs, D. R. Curtis, J. C. Eccles, *Nature* **178**, 1049 (1956).
5. P. Fatt, *J. Neurophysiol.* **20**, 61 (1957).
6. J. C. Eccles, *The Physiology of Nerve Cells* (Johns Hopkins Press, Baltimore, Md., 1957).
7. A. L. Hodgkin and W. A. H. Rushton, *Proc. Roy. Soc. (London)* **B133**, 444 (1946); L. Davis, Jr., and R. Lorente de N6, *Studies Rockefeller Inst. Med. Research* **131** 442 (1947).
8. A report of the mathematical treatment of this intermediate problem is in preparation.
9. W. Rall, *Proc. Univ. Otago Med. Sch.* **31**, 14 (1953), and abstract for National Biophysics Conference (1957).
10. L. G. Brock, J. S. Coombs, J. C. Eccles, *J. Physiol.* **117**, 431 (1952).
11. D. P. C. Lloyd, *J. Neurophysiol.* **9**, 421 (1946).
12. The opinions expressed in this note are my own, and are not to be construed as official or as reflecting the views of the U.S. Navy Department or the naval service at large.