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Voltage-controllable negative differential resistance in *Nitella translucens*

An investigation into the current–voltage characteristics of the plasma membrane of *Nitella translucens* has revealed a voltage-controllable negative differential

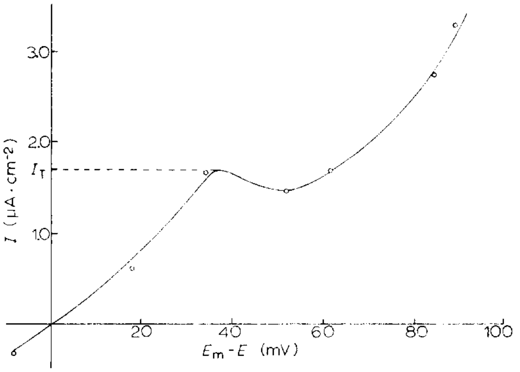

Fig. 1. Part of the steady-state current–voltage curve for *N. translucens* for hyperpolarising currents. The applied current (I) shifts the membrane potential from its normal resting value, E_m, to a new value E. The average value of E_m was close to −80 mV, the cells being bathed in 1.0 mM NaCl, 0.1 mM KCl, 1.0 mM $CaCl_2$. A regenerative transition occurs under constant-current conditions whenever the applied current amplitude exceeds the threshold current (I_T). The curve was plotted from data obtained from a series of potential responses to applied rectangular current pulses some of which are shown in Fig. 2.

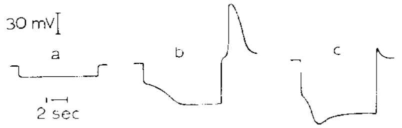

Fig. 2. Some membrane potential responses to applied rectangular current pulses. In (a) the applied pulse is sub-threshold and the response is capacitative with the membrane in its low-resistance state. In (b) the applied pulse is only slightly larger than threshold and about 1 sec after the beginning of the pulse the membrane commences to switch from the low-to the high-resistance state; following the break of the applied pulse an inductive potential transient occurs which triggers an action potential. Finally in (c) the applied pulse is well above threshold; in this case both the switching from low to high membrane resistance and the termination of the applied pulse are followed by an inductive membrane potential transient.

resistance in that region of the characteristic where the membrane potential is about 40 mV more negative than the resting potential (Fig. 1). The existence of a negative resistance region was inferred from the observation that membranes were capable of switching regeneratively between low- and high-resistance states (Fig. 2). The effect was clearly observed in about one third of the cells studied. The behaviour of the membrane is similar to that of the alga Valonia[1], frog nerve in isotonic KCl (ref. 2) and certain synthetic bilayer membranes[3].

In the present experiments, cells or cell sections shorter than 2.0 cm were used to ensure uniformity of applied current density, since it is known that the space constant for these cells lies between 2.0 and 4.0 cm (refs. 4, 5). Current was passed into a cell through a long, thin, 10 MΩ resistor, the internal current electrode being a pointed AgCl-coated silver wire. The internal potential-recording electrode was a conventional 3 M KCl-filled glass micro-electrode with a tip diameter less than 2.0 μ. Both electrodes were inserted transversely into the cell close to its mid-point.

For small applied currents the membrane resistance is usually between 10.0 and 30.0 k$\Omega \cdot$cm^2 (refs. 4, 5). However, at a well-defined threshold current (I_T), which can be as large as 2.0 μA$\cdot$cm^{-2}, the membrane resistance regeneratively increases. A two-fold increase in resistance was common but a three-fold increase sometimes occurred. Applied rectangular current pulses of amplitude less than I_T always gave rise to a capacitative membrane potential response with a time constant of about 40 msec, indicating that the membrane capacitance is between 1.0 and 2.0 μF$\cdot$cm^{-2} (ref. 4). Whenever the applied pulse amplitude exceeded I_T, the membrane potential response was inductive with a time constant of the order of seconds (Fig. 2). When the applied pulse strength was just equal to I_T, the potential transients observed as the membrane entered and left its high-resistance state were sometimes inductive and sometimes capacitative. As already mentioned, two thirds of the cells exhibited no well-defined resistance switching phenomena. Even so, these inexcitable cells all produced capacitative potential responses for low applied currents and inductive responses for higher applied currents, the threshold current for inductive responses being much the same as for the excitable cells. In all the cells studied it was observed that the inductive response of the membrane potential to the termination of a supra-threshold current pulse often gave rise to an action potential (anode-break excitation).

Voltage-controllable negative differential resistances invariably occur whenever two competing conduction processes interact by means of the electric field. For example, in the tunnel diode there is a field interaction between the diffusion current and the tunnelling current[6], while in Gunn effect crystals the interaction takes place between the conduction band electron current and a "hot" electron current in a higher band[7]. It has been suggested that two types of interacting K^+ conducting channels are responsible for the negative resistance in synthetic bilayer membranes[3]. This explanation is probably valid for Nitella, though it will be difficult to prove that the interacting currents are K^+ currents because the ion-exchange properties of the cell wall can so easily distort the effect on the membrane potential of changes in the ion concentrations of the environmental solution[8]. The fact that the membrane in its high-resistance state produces an inductive response to applied current pulses may furnish a clue as to the nature of the two types of ionic conduction processes in the membrane. Analysis of several membrane equivalent circuits indicates that a membrane energy-storage element corresponding to an inductance of the order of 10^5 H·cm^2 is required to explain the observed results. This energy-storage mechanism is undoubtedly directly related to the ionic conduction mechanism in the high-resistance state. At present, however, there is little experimental evidence to suggest what these mechanisms might be in molecular terms except that they are probably connected with membrane protein[9]. It is perhaps relevant to remark that the phenomenon of membrane inductance has been observed in the squid axon[10]. A quantitative analysis[11] suggests that it arises largely as a result of changes in the K^+ conductance of the membrane.

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