MATTERS ARISING

BVP models of nerve membrane

HINDMARSH and Rose¹ propose, for use in simulating networks containing small numbers of neurones, a phenomenological model based on their experimental data, and notable for its simple numerical integrability. Inspection of their paper shows that their experimental data do not in fact extend into the region $x < -15$ mV, yet it is just this region that contains the novel feature of their model, a positive gradient for the isocline $\dot{y} = 0$. Others (for example, see ref. 2) have collected data in this region which do not support the positive gradient used by Hindmarsh and Rose for $\dot{y} = 0$ (see Fig. 1). Thus, their slow variable y has less physical meaning than the usual BVP (Bonhoeffer-van der Pol) slow variable³. Furthermore, for constructing models of this kind, there already exists a method^{4,5} which gives explicitly solvable equations and requires no numerical integration. Over the full range of experimental data, this method gives a better fit than that of Hindmarsh and Rose. The method is as

follows: divide the voltage range into three segments; fit the data in each segment with a straight line (making $f(x)$ and $g(x)$ continuous and step-wise linear); and solve the resulting second-order linear system of ordinary differential equations.

Real nerve cell membranes, the Hodgkin-Huxley system⁶, and the usual BVP models⁴ are made relatively more excitable by an anode break shock. In contrast, its novel feature makes the Hindmarsh-Rose model relatively refractory after such a stimulus.

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HINDMARSH AND ROSE REPLY—The novel feature we wished to draw attention to was not the positive gradient of the isocline $\dot{y} = 0$ in the region $x < 0$, but rather the close proximity of the isoclines $\dot{x} = 0$ and $\dot{y} = 0$. This proximity is determined by $z_{sp}(\infty)$, which is small according to both the Hodgkin-Huxley data for x_p between 0 and -65 mV and our data for x_p between 0 and -20 mV. On the other hand, the location of these isoclines is determined by $z_{sp}(0)$. Few points were obtained for $z_{sp}(0)$ for $x_p < 0$ because by using the single electrode voltage clamp, the initial responses were obscured by a capacitive current. We therefore followed Fitzhugh¹ in taking a cubic form for $z_{sp}(0)$. Due to this, both isoclines have a positive gradient in the region $x < 0$ which, as both Game and Fitzhugh (personal communication) have pointed out, means that our model is relatively refractory after an anode break shock. Although this positive gradient is thus a disadvantage in our model, it is consistent with the following experiment (tail current reversal) performed numerically with the Hodgkin-Huxley² equations.

If the voltage is held at +50 mV until a steady state is reached, and then stepped back to various negative potentials, it is found that when the potential is sufficiently negative, the tail current changes direction. This property is shown, at least qualitatively, by our model, as can be seen from our phase plane diagram³. Given the choice between explanations of tail current reversal or anode break, we chose the former, because we saw that this would also predict the long interspike interval. This suggests that $z_{sp}(0)$ for $x_p < 0$ should be constructed from such

tail current data rather than from negative voltage steps from zero. Such a determination seems more relevant to the time course of the membrane potential during firing.

Clearly, if $z_{sp}(0)$ is determined from voltage clamp steps from zero and the Hodgkin-Huxley data is used (Fig. 1a), then straight lines will provide a better fit than a cubic. In this case both isoclines will still have a small positive gradient in the region $x < 0$, which will mean that the phase state on the limit cycle travels far to the left before returning to the origin between the isoclines, resulting in a large undershoot of the membrane potential. In our case, replacing the cubic by three straight lines does not lead to a significant deterioration in accuracy of prediction of the time course of the membrane potential, and does, as Game points out, offer the advantage of explicit solutions.

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Trophic structure of a grassland insect community

FROM a detailed study of insect species in a grassland community, Evans and Murdoch¹ concluded that the ratio of herbivorous insects to entomophagous insects remained fairly constant throughout the growing season. They suggested that this reflected an underlying trophic pattern that persisted despite continuing turnover of species. Cole² rejected this claim by showing that an appearance of constancy can be generated by samples taken from a fixed pool of all available species.

It is true that in the absence of exact knowledge of the community structure through the season it is not possible to assert that species turnover occurs. However, it is equally impossible to assert that species turnover does not occur. Nevertheless, this is precisely the arbitrary assumption made by Cole.

He assumes that all species listed by Evans and Murdoch (131 herbivorous, 80 entomophagous) are present throughout the season, and treating the total number of species observed each fortnight as a random sample (r) from the population of 211 species, he demonstrates that the expected number of herbivores agrees

Fig. 1 Schematic summary of the data under consideration. Ordinates show the membrane current supplied by the clamping electrode; the abscissae show the membrane potential at which the clamp is set. ○, Steady-state current; ●, initial current. a, Based on the data of ref. 2 for squid giant axon; b, based on the data of ref. 1 for snail neurone soma.