AXONAL INFORMATION PROCESSING

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ABSTRACT

A piecewise linear model of the membrane is used in a transmission line model of the axon. This allows an expression for the propagation velocity of action potentials to be derived. It is shown that action potentials "interact" and that this expression plays a key role. For axons with larger length/diameter ratios, the pulse pattern emanating from the soma is changed when it arrives at the synaptic knobs.

INTRODUCTION

In considerations of nervous information processing it has often been overlooked that signals generated on the soma of the nerve cell are not reproduced (with an appropriate time delay) at the distal end of the axon. Although the individual action potentials with their all-or-none behaviour do not vary much in size and shape, it is found that the propagation velocity is rather sensitive to the state of the axon and its environment. This state changes with the presence of action potentials (other than the one considered) ahead or on adjacent axons. The usually considered propagation velocity is the velocity of a single action potential travelling alone on an axon in a passive, field-free medium. In this paper we shall consider the velocity dispersion due to after-effects only, not the effect of stray fields from surrounding cells. Bullock[1] has described the "facilitation of conduction rate" in 1951; However, functional relationships to axonal parameters have not been established. Were this to be done by means of e.g. the Hodgkin-Huxley equations[3], it would mean exceedingly cumbersome computations. In this study we utilize a much simpler model of the membrane. Given certain data about the after-effects we are then able to predict the variations in propapation velocity.

THEORY

The model[2] is a piecewise linear transmission line. It has the following characteristics:

1. Resting state potential
2. Threshold voltage
3. Resting state conductance
4. Peak sodium conductance.

It can be shown that, as far as the propagation velocity is concerned, these four parameters are the most essential. The model describes the rising phase of the action potential only, not the recovery to the resting state. Because the spike of the action potential is associated with virtually a short circuit (in the form of greatly increased sodium conductance), these later events cannot influence the parts in front of the spike appreciably. They therefore do not contribute to the propagation velocity of the action potential. The recovery phase is, on the other hand of direct consequence to the subsequent action potential which "sees" different line parameters ahead of itself. It is not surprising that we have this interaction between the spikes considering

the fact that the transmission line is highly nonlinear. For the model we find[2]

$$\theta = \frac{1}{2C_M}\sqrt{\frac{g_{Na}^{max}}{\rho}}\;\frac{\beta^2 - g^\circ/g_{Na}^{max}}{\sqrt{\beta(1-\beta)(\beta - g^\circ/g_{Na}^{max})}}\sqrt{d}$$

where:

θ = propagation velocity
C_M = membrane capacitance
g_{Na}^{max} = specific Na conductance, max.value
ρ = specific resistivity of axoplasm
g° = specific resting state conductance
β = normalized threshold = V_T/V_o
V_o = resting state voltage
V_T = threshold voltage
d = axon diameter.

For the Hodgkin-Huxley squid giant axon[3] we find the nominal velocity θ = 25.1 m/sec with the following values of the parameters: V_o = 115 mV, V_T = 115 - 35 = 80 mV, β = 0.696, C_M = 1.0 μF/cm^2 ρ = 35.4 ohm-cm, g° = 0.54 mmho/cm^2, g_{Na}^{max} = 25 mmho/cm^2, d = 0.0238 cm.

VELOCITY DISPERSION

The value of the expression above lies in the fact that it gives the propagation velocity θ in terms of measurable (and easily conceivable) parameters of the axon. Suppose we have a long axon on which an action potential travels with the nominal velocity, corresponding to the undisturbed case. In its wake it leaves afterpotentials and afterconductances, i.e. non-equilibrium values of these quantities. If a second action potential happens to fall somewhere in this interval with aftereffects the expression above tells us that the velocity of that second spike will be different. In the case of the H-H axon we find the relationship in Fig.1.
Fig. 2 shows experimental curves measured by Bullock[1] on different preparations. Observe the striking similarity to Fig.1.

PULSE PATTERNS

A given spike train will change as it travels along an axon, in particular for axons with large length/diameter ratios. The data shown in Fig.1 can be integrated to show the changing spike distance versus elapsed travel time. It is noticed that there is a tendency for the spikes to "lock" at certain distances. In this case the second spike seeks to assume a position 6 msec or approximately 15 cm after the first one.

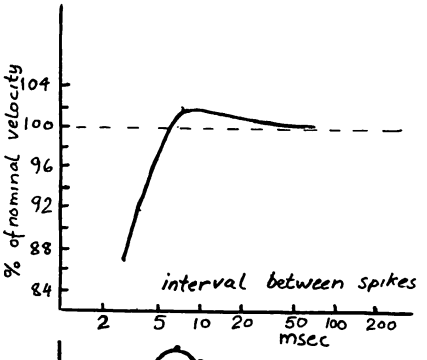

Fig.1

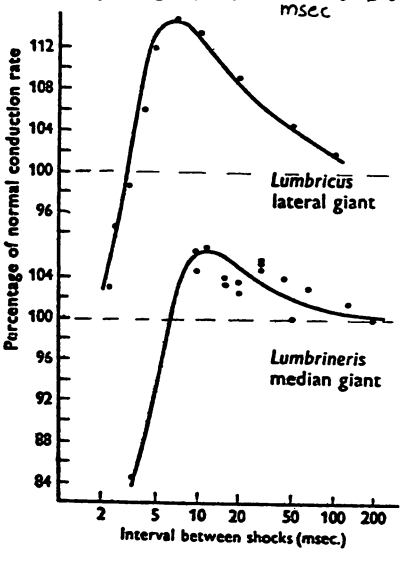

Fig.2 after Bullock[1]

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