Probabilistic Models for Determining the Input-Output Relationship in Formalized Neurons

I. A Theoretical Approach

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Abstract. In order to investigate under which assumptions one can expect to determine the probabilistic response of a neural unit to an incoming stochastic excitation, we propose a model that endows the neuron with a variable threshold. It is shown that a fairly complete statistical description of the input-output relationships can be obtained when the input is Poisson, non-homogeneous Poisson and, finally, any stationary continuous stochastic process.

1. Introduction

Preliminary to any attempt at formalizing the dynamics of a nervous system is the choice of the level at which it is appropriate to do it. This immediately leads to a certain number of fundamental questions that in turn, because of the very poor knowledge of the phenomena involved in the "activity" of nervous systems, are in danger of remaining in the world of metaphysics. Nevertheless, interesting (though less ambitious and therefore better stated) problems have often arisen, and functional models accounting for the role played by specific portions of nervous systems have been proposed in the literature: It will suffice here to recall the classical paper by Reichardt on the visual responses of the Chlorophanus [1] and the Braitenberg's anatomo-functional model of the cerebellum [2]. An extensive critical review of the literature on modelling nervous systems, still lacking at present, is a very appealing task for the cybernetician, as it would provide some of the hints necessary in order to figure out a useful and appropriate level for studying the dynamics of a nervous system as a whole.

Although we are aware that this latter is the most relevant problem in theoretical biology (certainly it is the most fascinating one), in this paper we will be concerned with a much less ambitious task, consisting of the description, in a probabilistic fashion, of the input-output relationship for a physical system that strongly reminds us of the neuron as first envisaged by McCulloch and Pitts [3]. Whether this, and the many similar attempts already existing in the literature, will eventually represent a contribution to the more general problem mentioned before is still an open question that will not be discussed here.

It is not at all clear whether the probabilistic approach to the study of a single neural unit is the only possible one. Sometimes, using a deterministic model for the neuron's activity may lead to straightforward explanation of some experimental data [4], although the well known variability in the firing intervals under constant external stimuli, always observed in complex neuronal systems, ought to be better accounted for if one makes use of stochastic models for the repetitive activity of neurons. This circumstance, however, should not lead to the superficial conclusion that the neuron's activity is indeed regulated by probabilistic laws: It simply means that, at present, statistical models seem to be able to furnish a better description of the observable neuron's activity.

Since after the classical paper by Hagiwara [5], many articles have appeared aiming at the interpretation of electrophysiological traces, obtained in intracellular recording experiments, and at the formulation of models for the neuron's activity able to account for some of the statistical features presented by the recorded data (see, for instance, Refs. [6, 7] and further references therein); very often, because of the mathematical difficulties that arise in these kinds of problems, computer simulations have been used.

Out of the several possible ways of formalizing the macroscopic behavior of a neural cell we will consider a rather simple-minded one that, nevertheless, was already proved to enable us to solve some interesting problems [8-10]; we will make this model more adherent to what appears to be the real situation by introducing in it a time-variable threshold, of the type pointed out in Ref. [5]. That, in turn, accounts for the existence of a relative refractoriness after each spike produced by the model neuron.

The obvious advantage of using a rather simple model for the neuron consists in the possibility of describing in a complete fashion the output when the input is assigned: increasing too much the complexity of the unit does not seem to be worthwhile for the time being because, after all, the big unknown that prevents a straightforward fitting of the experimentally recorded traces with the theoretically predicted results is the physiological input that a real neuron receives from both the external environment and the rest of the complex net to which it generally belongs. Using a simple model may allow us to solve the input-output problem for a rather large class of neural stimuli, so that one can hope that, at least in some instances, the real excitation impinging on a neuron will belong to such a class, thus making meaningful a comparison of theoretical predictions and experimental data.

Denoting by \( u(t) \) the all-or-none state of the neuron at time \( t \), by \( S(t) \) its threshold and by \( E(t) \) the total excitation impinging on it, we will assume the following state equation to hold [8-10]:

\[
\frac{1}{\lambda} u(t) = 1[ E(t) - S(t) ],
\]

(1.1)

where \( 1(x) \) denotes the Heaviside unit step-function, defined as:

\[
1(x) = \begin{cases} 1, & x > 0 \\ 0, & x \leq 0 
\end{cases}
\]

(1.2)