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Computers in Biology and Medicine 35 (2005) 85–90

<http://www.intl.elsevierhealth.com/journals/cobm>

Computers in Biology
and Medicine

Neurons with radial basis like rate functions

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Received 23 May 2003; received in revised form 29 October 2003; accepted 29 October 2003

Abstract

Artificial neural networks constructed with “locally tuned processing units” and more generally referred to as “radial basis function networks” have been proposed by a number of workers. In this communication, I submit a conjecture, based on indirect experimental and direct computational evidence of the Hodgkin–Huxley model, that there may be biological neurons in nervous systems for which the rate function is locally tuned. If proved to be valid, this conjecture may simplify neurodynamic models of some functions of nervous systems. © 2003 Elsevier Ltd. All rights reserved.

Keywords: Computational neuroscience; Computer simulation; Electrophysiology; Modelling; Neurophysiology; Radial basis neural networks; Spiking neurons

1. Introduction

In the early stages of experimental electrophysiology, it has been established that the firing frequency of neurons may be the most significant variable for coding stimulus intensity [1]. This principle of “frequency coding” has since become an important paradigm for modelling peripheral, as well as some central functions in the nervous system. Plenty of direct, clear-cut experimental evidence has been accumulated to support this principle at least as a first approximation. The accumulated data stress the fundamentally monotonic and saturating relationship between the firing rate and the stimulus intensity, which may be expressed in terms of generator potentials or membrane depolarisations. This fact has eventually been synthesised for analytical and modelling purposes by the class of sigmoid functions of which the logistic function $f(x) = \alpha/(1 + \exp(-\beta x))$ turned into the most popular one. In this paper, I propose that some neurons in nervous systems may have non-monotonic rate functions such as the radial-basis functions [2,3]. To support this hypothesis I

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submit indirect experimental evidence taken from the literature, plus direct computational evidence based on the Hodgkin–Huxley model, for the genesis and propagation of the action potential. Finally, I point out that dynamic networks of such neurons may provide interesting possibilities for modelling in much simpler and biologically plausible ways certain functions of the nervous system.

2. The rate function

In primary sensory nerve fibres, the rate function expresses the relation of the action potential firing frequency to stimulus intensity, which is either measured directly or through its associated generator potential. For other neurons, the rate function expresses the dependence of firing frequency on the depolarising membrane potential at the axon hillock. Firing rates have been measured over several decades for most of the peripheral sensory and motor modalities as well as for other neurons in vivo and in vitro. The overwhelming majority of these measurements focused on the “dynamic” or “working” range of stimulus intensity, over which the firing rate grows monotonically before saturating at some maximal level. However, some of these studies were extended to the *supramaximal* stimulation levels. A closer examination of these results indicates that the firing rate, after staying constant for a while at roughly its maximum value, instead of dropping abruptly to zero, follows a relatively smooth and regular trajectory, with the frequency decreasing at rates of the same order of magnitude as the ones observed over the “working” range. Figs. 1(a) and (b) show two of such rate functions published in the literature.

The rate function has also been studied in silicium, that is through computational simulations of the dynamic equations that underlay the production and conduction of the action potentials in nerve fibres. In computational simulations of the point-polarised propagated Hodgkin–Huxley equations, Stein [4] obtained a similar result, shown in Fig. 1(c).

3. Simulation model

Since all three curves shown in Figs. 1(a)–(c) contain relatively scarce data on the supramaximal stimulus range, I computationally simulated the propagating Hodgkin–Huxley equations [8] under the following circumstances: (1) the voltage-dependent rate constants α_m , β_m , α_h , β_h , α_n and β_n were the original ones provided by the Hodgkin–Huxley model; (2) membrane capacitance was $1 \mu\text{F}/\text{cm}^2$, $g_{\text{leak}} = 0.1 \text{ mS}/\text{cm}^2$, $E_{\text{leak}} = -30 \text{ mV}$; $\bar{g}_{\text{Na}} = 100 \text{ mS}/\text{cm}^2$, $\bar{g}_{\text{K}} = 80 \text{ mS}/\text{cm}^2$, $E_{\text{Na}} = 50 \text{ mV}$ and $E_{\text{K}} = -90 \text{ mV}$. Furthermore, the membrane potential at the axon hillock was considered as a randomly fluctuating signal about a mean value, to account for the fact that is the result of the spatial and temporal integration of all incoming synaptic activity. This was modelled by a low level, uniformly distributed membrane noise with a SNR = 40 dB. The propagation model was of the multicompartmental type [8], since intercompartmental currents are important to control repetitive firing [9]. The coupling coefficient between compartments was chosen to be consistent with a propagation velocity of 20 m/s and the average pulse rate was calculated over a period of 400 ms after propagating five compartments. Actually, after three compartments the time structure of the pulse train remained unchanged except, of course, for a progressive delay consistent with the fibre conduction velocity. Consistently with Stein’s results and with the direct experimental observations made for

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