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Low correlation between random synaptic inputs impacts considerably on the output of the Hodgkin–Huxley model

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Abstract

The effects of positive and negative correlation, c, between ($N = 100$) random synaptic inputs (each firing at 100 Hz) on the mean and coefficient of variation (CV) of interspike interval (ISI) of the Hodgkin–Huxley model are examined, for different IPSP/EPSP frequency ratios, r. Mean (ISI) and CV are approximately constant (30–40 ms, and 0.75, respectively) under independence for $r \in [0,1]$, unlike the leaky I&F model. Low positive correlations ($c \simeq 0.1$) reduce mean ISI and CV up to threefold to the regular firing range; small negative correlations ($c \simeq -0.005$) double mean ISI and increase CV by 25%. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Correlation; Stochastic synaptic input; Hodgkin–Huxley model; Synaptic balance

1. Introduction

Many neurons fire irregularly when driven weakly by random synaptic input, but quite regularly when driven very hard. Between these extremes, neurons differ in their response to random input. Previous work of ours [1,3] has shown that for the leaky integrator, CV falls in the physiological range (between 0.5 and 1) for a range of values of r, the ratio of the frequencies of inhibitory to excitatory input, the range being wider when reversal potentials are excluded. The behaviour of the classical Hodgkin–Huxley (HH) model of squid giant axon is very different in that it can fire quite

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irregularly over the complete range of r, unlike the leaky $I\&F$ model, which fires regularly when inhibitory inputs are absent. In this paper, we examine how mean(ISI) and CV(ISI) change when the synaptic input streams are no longer independent but correlated with a uniform correlation between all pairs of inputs. We demonstrate that such correlations can change the firing pattern and rate very substantially, in a manner which is rather different from the leaky integrator.

2. Model

The Hodgkin–Huxley model and parameter values used are as described in [5]. Zohary et al. [6] obtained average correlation coefficients between spike counts in simultaneously recorded neurons in the middle temporal visual area of 0.12. We therefore consider here the case of $p = 100$ excitatory inputs each of 100 Hz with a maximum correlation of 0.1, and $q = rp$ inhibitory inputs, for r between 0 and 1. The correlation between each pair of inputs is the same for all pairs, though there is independence between the inhibitory and excitatory inputs as groups. In the case of negative correlation we only consider departures from independence as small as $c = -0.01$.

We used a diffusion approximation to model the correlated Poisson point process input. This approximation in the case of independent Poisson point process input to a Hodgkin–Huxley model has been shown to be adequate [2]. By this means, the effects of the Poisson synaptic input are transformed to a form more convenient for computer simulation. The approximations of the excitatory and inhibitory components of the synaptic input,

$$I_{\mathrm{syn}} = \mathrm{d}E_i(t) + \mathrm{d}I_i(t)$$

are

$$\mathrm{d}E_i(t) \sim \lambda_{\mathrm{E}}\mathrm{d}t + \sqrt{\lambda_{\mathrm{E}}}\mathrm{d}B_i^{\mathrm{E}}(t)$$

and

$$\mathrm{d}I_i(t) \sim \lambda_{\mathrm{I}}\mathrm{d}t + \sqrt{\lambda_{\mathrm{I}}}\mathrm{d}B_i^{\mathrm{I}}(t),$$

where $B_i^{\mathrm{E}}(t)$ and $B_i^{\mathrm{I}}(t)$ are standard Brownian motions. Thus, synaptic input can be approximated by

$$I_{\mathrm{syn}} = a\sum_{i=1}^{p} \lambda_{\mathrm{E}}\mathrm{d}t - b\sum_{i=1}^{q} \lambda_{\mathrm{I}}\mathrm{d}t + a\sqrt{\lambda_{\mathrm{E}}}\sum_{i=1}^{p} \mathrm{d}B_i^{\mathrm{E}}(t) - b\sqrt{\lambda_{\mathrm{I}}}\sum_{i=1}^{q} \mathrm{d}B_i^{\mathrm{I}}(t). \tag{1}$$

Since the sum of Brownian motions is also a Brownian motion, we can rewrite the above equation

$$I_{\mathrm{syn}} = (ap\lambda_{\mathrm{E}} - bq\lambda_{\mathrm{I}})\,\mathrm{d}t + \sqrt{a^2p\lambda_{\mathrm{E}} + b^2q\lambda_{\mathrm{I}} + a^2\lambda_{\mathrm{E}}cp(p-1) + b^2\lambda_{\mathrm{I}}cq(q-1)}\,\mathrm{d}B(t). \tag{2}$$

3. Results

Mean and coefficient of variation of ISI (CV in what follows) for the HH model change substantially as the simultaneous synaptic inputs become positively and negatively correlated, even if only slightly. As the pairwise correlation between these inputs increases to 0.1, mean ISI falls to between a third and a half of its value under independence, and CV falls to about one third of its independence value (Fig. 1,

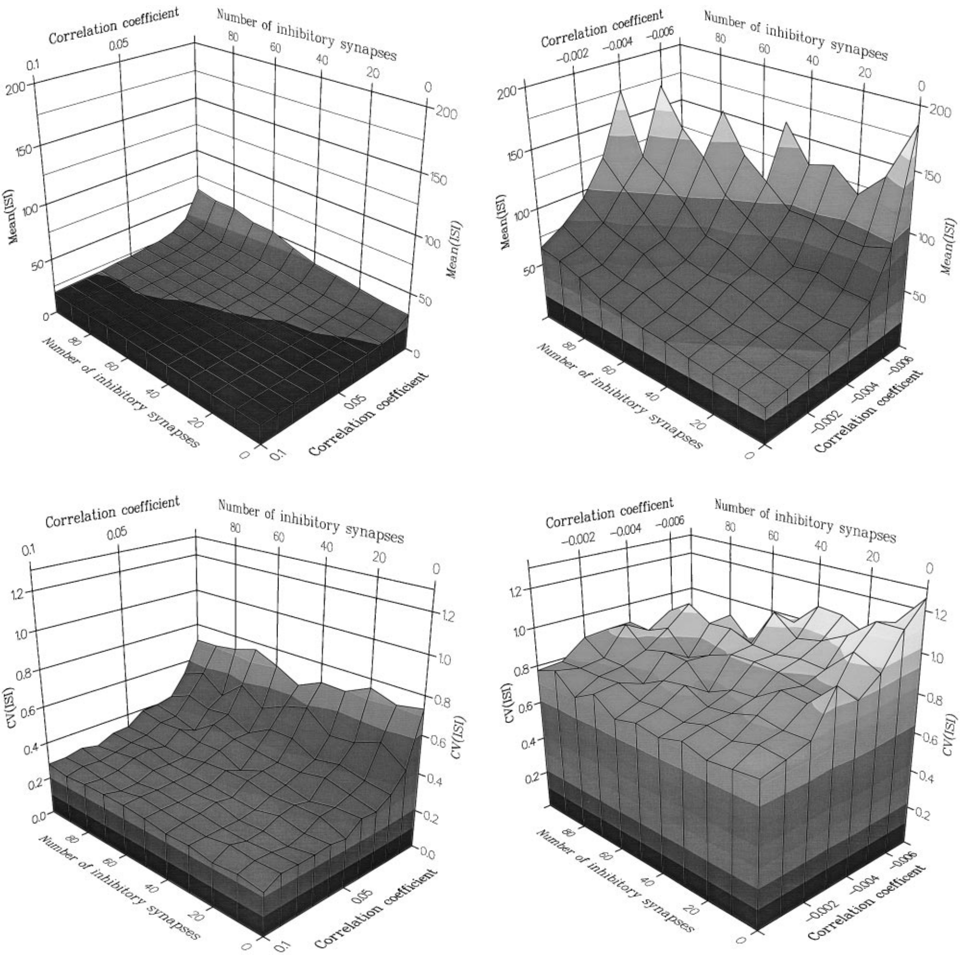

Fig. 1. Mean firing time(upper) and CV(lower) of the ISI output of the HH model subject to $p = 100$ excitatory EPSPs arriving according to Poisson processes, with EPSPs of amplitude 0.5 mV, and $q = rp$ inhibitory inputs also Poisson distributed, with correlation, c, between the 100 excitatory (and $100r$ inhibitory) processes lying between 0 and 0.1 (on the left), and between 0 and -0.01 (on the right) as indicated on the axes. The model is simulated using the approximation to Poisson input as described in the text.

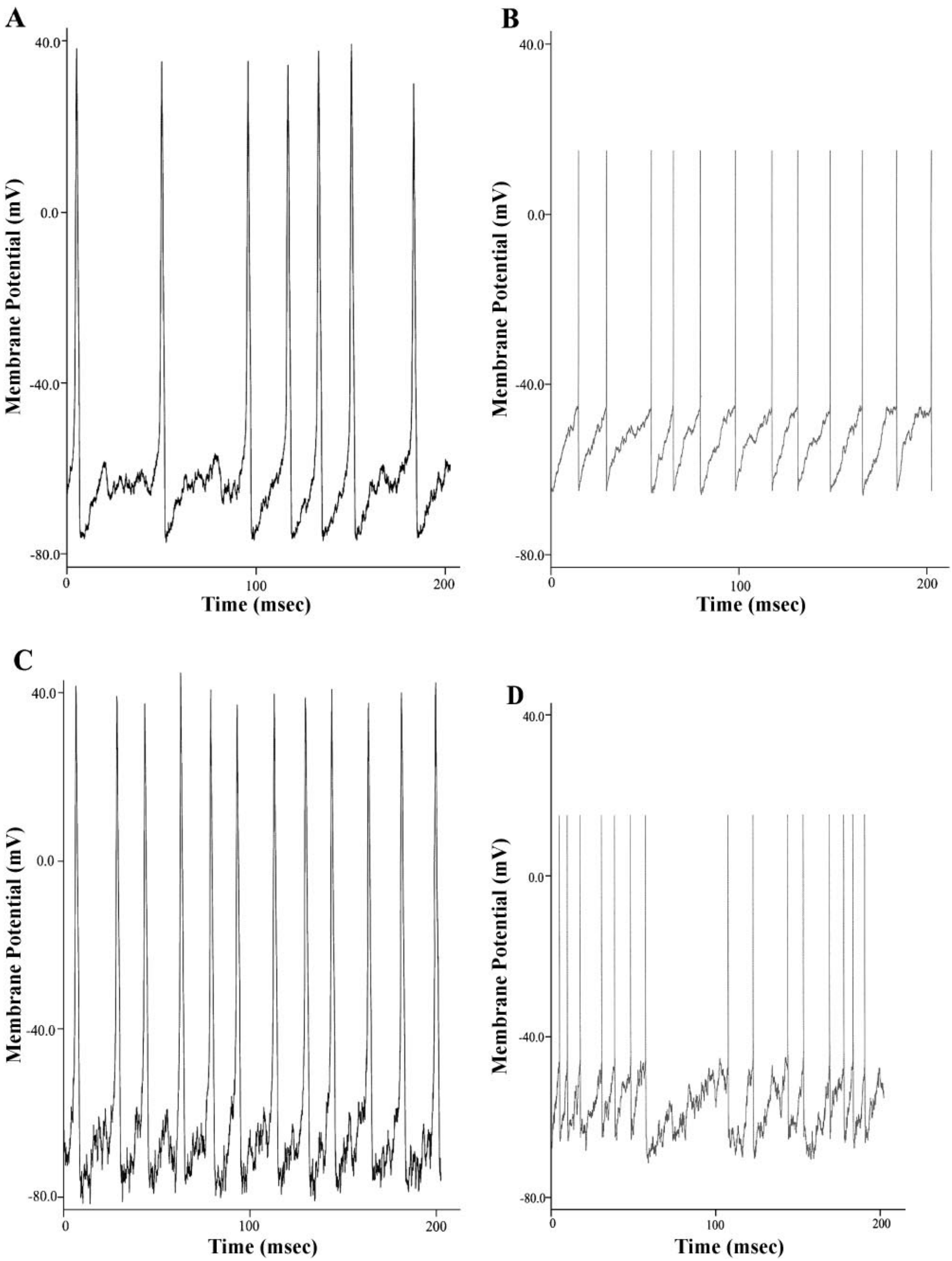

Fig. 2. Typical output firing pattern of the HH model subject to $p = 100$ excitatory EPSPs arriving according to Poisson processes, with EPSPs of amplitude 0.5 mV, and $q = rp$ inhibitory inputs also Poisson distributed, with correlation, c, between the $p = 100$ excitatory (and $q = 100r$ inhibitory) processes for (A) independent inputs, $c = 0$, and (C) correlated inputs, $c = 0.1$. For comparison, simulations of the leaky integrator model with decay time 20 ms, EPSP and IPSP size 0.3 mV, are given for (B) independent inputs, $c = 0$, and (D) correlated inputs, $c = 0.1$. The models are simulated using the approximation to Poisson input as described in the text.

left-hand side); that is to say, the neuron fires much faster and much more regularly.

For negative correlations, the effects are more marked and involve much smaller departures from independence. For correlations smaller than -0.01 in absolute magnitude ($r \simeq -0.008$), the activity of the HH neuron falls almost to zero (Fig. 1, right-hand side). Mean (ISI) approximately doubles over the whole range of r for $c \simeq -0.005$, and CV increases by about 25% over this range.

4. Discussion

The reason why small correlations have such a profound effect can be seen by examining the diffusion approximation we used in the computer simulations: there are $p(p-1)$ covariance terms in the expression for I_{syn} in Eq. (2), so that the covariance contribution increases much faster than p, even though the multiplier of $p(p-1)$, i.e. the correlation, is rather small. Furthermore, the effect of these changes in correlation are quite different in kind from those which occur with the leaky I&F model [4]. For this model, the effects of positive correlation in synaptic input are to increase CV and mean(ISI), rather than reduce them as here. See Fig. 2 for typical comparative simulations of these cases.

Finally, what are the implications of these findings for neuronal coding? Adjusting the degree of correlation between inputs could be easily accomplished by a neural network; for example, an increase could occur by increasing the impact of common inputs. We have seen here that small departures from independence — equal to or smaller than those found in visual cortex [6] — can have very big effects on both the rate of variability of firing of individual neurons. The effects depend strongly on the nature of the neuronal mechanism, as demonstrated by comparing the present findings with those in [4]. These results suggest that population coding in networks composed of different neuronal types could be a very flexible communication mode in neuronal systems.

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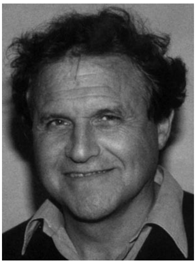
References

[1] D. Brown, J. Feng, Is there a problem matching real and model CV(ISI)? Neurocomputing 26-7 (1999) 87–91.
[2] S. Feerick, J. Feng, D. Brown, Random pulse input versus continuous current plus white noise: are they equivalent? Neurocomputing (2000), in press.
[3] J. Feng, D. Brown, Coefficient of variation of interspike intervals greater than 0.5. How and when? Biol. Cybernet. 80 (1999) 291–297.

[4] J. Feng, D. Brown, Impact of correlated inputs on the output of the integrate-and-fire model, Neural Comput. (2000), in press.
[5] A.L. Hodgkin, A.F. Huxley, A quantitative description of membrane current and its application to conduction and excitation in nerve, J. Physiol. 117 (1952) 127–153.
[6] E. Zohary, M.N. Shadlen, W.T. Newsome, Correlated neuronal discharge rate and its implications for psychophysical performance, Nature 370 (1994) 140–143.



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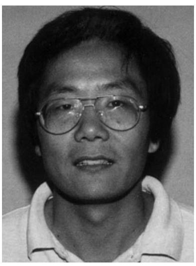

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