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## **RELIABILITY OF SPIKE ENCODING IN CORTICAL NEURONS**

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There have been many recent articles on the coding properties of nerve cells, with emphasis on the precision and reliability of the processes involved<sup>1-7</sup>. In our investigations of stochastic effects in nonlinear biological neuron models<sup>8</sup>, we have examined especially some results obtained on the firing properties of certain neocortical cells<sup>3</sup> in which various currents were injected repetitively and the accompanying sequences of spike times were recorded. An interesting and seemingly paradoxical result was obtained: when a constant current was injected into the cell, a spike train was obtained which became more variable with time, whereas when a variable current waveform was repeatedly injected, practically identical spike trains were obtained in each trial. It thus seemed that variability somehow led to greater reliability because a constant input current (here called case A) led to a noisy output whereas a noisy input (here called case B) led to a fixed output pattern.

However, we have found with realistic nonlinear conductance-based neural models that these apparently paradoxical results are readily explained and

that greater variability in the input can, except in perhaps some special situations, only ever lead to greater variability in the output of a nerve cell. We use the usual convention of small letters for deterministic quantities and capital letters for random ones. In A let the constant input current have magnitude  $i_1$  and in B let the noisy input waveform be  $i_2(t)$ . Although the latter was obtained from a random generator, it was in fact deterministic as the same wave form was repeatedly presented. The average value of  $i_2(t)$  during the stimulus presentation was  $i_1$ . Although there were attempts to suppress stochastic synaptic inputs, these were still present <sup>9</sup> and may be represented by a random current source  $N(t)$ . In case A the current was supposedly  $i_1 + N(t)$  and in case B,  $i_2(t) + N(t)$ . However, the application of a sustained depolarizing current ( $i_1$ ) switches on inward hyperpolarizing currents  $i_K(t)$ , usually attributed to potassium, which are one cause of adaptation <sup>10</sup>. Thus in case A the actual current was  $I_A(t) = i_1 - i_K(t) + N(t)$  whereas in case B it was  $I_B(t) = i_2(t) + N(t)$ . Furthermore, because the stimulating currents were applied repeatedly for 25 trials, the absolute value of  $i_K(t)$  continued to grow not only within a given trial but also from one trial to the next, making the deterministic component of  $I_A(t)$  grow smaller and smaller. Now in case B it is evident from the results that  $N(t)$  was relatively small so that when the same waveform was presented 25 times, the sequence of spike times was practically the same. It is emphasized that even though  $i_2(t)$  was produced by a random generator, it was in fact nonrandom and because  $N(t)$  was relatively small,  $I_B(t)$  was also essentially deterministic. However, in case A, the deterministic component of the current,  $i_1 - i_K(t)$ , continually decreased throughout the experiment so that the noise  $N(t)$  became more and more dominant. These factors led in case A to the observed increase in the mean output interspike interval and the increase in its variability. The results thus lose their paradoxical nature because in case A where the input current seemed constant it was in fact growing smaller in mean value and greater in its noise to signal ratio; whereas in case B, the input was fluctuating (non-steady) and deterministic with a very small stochastic component. Thus, the results were compatible with the usually found increase in output variability in response to a more

variable input current <sup>11</sup>. The reliability of nerve cell encoding, in the sense that the same *overall* input current leads, given no change has occurred in the parameters of the cell or its immediate environment, to practically the same output sequence of spike times remains true, as found in neocortical cells <sup>3</sup> and other preparations <sup>12</sup>.

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