

Information Transmission and Temporal Code in Central Spiking Neurons

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The brain encodes information in the intervals between the spikes which characterize neural firing events. Therefore it is relevant to study, in a timing code, how many spikes are necessary for reliably encoding input signals. We analyze the transmission of information, the reliability of signal detection, and the coding strategy for the case of central spiking neurons. [S0031-9007(97)04697-8]

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A major challenge in neurobiology is the question of how information is encoded and transmitted in the neurons. It is generally agreed that the brain encodes information by the action potentials or “spikes” which characterize neural firing events [1,2]. Historically, the first proposal of a code mechanism was made by Adrian [3]. It corresponds to the observation that, in response to a static stimulus such as a continuous load on a stretch receptor, the rate of spiking increases as the stimulus becomes larger. Hence, the rate of spikes encodes the intensity of the stimulus. This is widely known as *rate coding*. In other words, the idea is that the mean firing rate alone encodes the signal, while the variability about the mean is noise [4]. Softky and Koch [5] have shown that the spike trains of cortical cells in the visual areas V1 and MT display a high degree of variability. This variability is characterized by the coefficient of variation $CV = \sigma_{ISI}/\mu_{ISI}$, where σ_{ISI} and μ_{ISI} are the standard deviation and mean value of the interspike intervals (ISI), respectively. Cortical cells have CVs in the range 0.5–1.0 as reported by Softky and Koch [5]. Thus, these authors suggested that high ISI variability may be more consistent with Abeles’ [6] idea of neurons acting as *coincidence detectors* rather than rate encoders. An alternative philosophy is to consider that it is variability itself that encodes the information contained in the input signal [7]. This concept corresponds to the notion that the precise sequences of time in which the spikes are emitted encodes the signal, yielding a *timing coding*. Experimental studies [2,8,9] support this concept. Therefore, it is relevant to study in a timing code how many spikes are necessary for reliably encoding input signals. The appropriate framework to investigate this problem from a theoretical point of view is provided by information theory [2,10,11]. The purpose of this paper is to analyze by use of information-theoretic concepts the transmission of information, the reliability of signal detection, and the coding strategy for the case of central neurons.

We first consider an integrate-and-fire model of a central neuron which combines diffusion and jump processes. This is motivated by experimental and theoretical studies which demonstrate that the effect of synaptic input on neural excitability decreases with the distances between the synapse and the cell body, where spike generation is

initiated. Somatic synapses cause changes in the membrane potential which are a large fraction of the threshold depolarization, while signals impinging on the periphery of an extensive dendritic tree evoke small potential changes at the soma. The changes induced by the inputs in the dendritic tree structure are well described by the continuous approach of Stein which is given by the Ornstein-Uhlenbeck diffusion process used in neural modeling [1]. The model combining diffusion and jump process can be expressed by the Itô-type stochastic differential equation

$$dV(t) = \left(-\frac{V(t)}{\tau} + \mu \right) dt + \sigma dW(t) + w dS(t). \quad (1)$$

In Eq. (1), $dW(t)$ is a standard Wiener process. The constant τ describes the decay of the membrane potential in the absence of input signals. Here, $S(t)$ is a homogeneous Poisson process, i.e., $s(t) = \frac{d}{dt}S(t) = \sum_i \delta(t - t_i)$, where the t_i are Poisson distributed random instants with mean rate λ (i.e., the mean value of the time interval between events is λ^{-1}). The soma-synaptic strength is denoted by w and the mean value by μ which is taken equal to zero. A spike is generated when the membrane potential $V(t)$ reaches a prefixed threshold θ . After the generation of the spike, the model is reset to a given initial potential $V(0)$ (in this paper, it is taken to be equal to zero). The output spike train is therefore described by the spike generation times t'_0, \dots, t'_k, \dots , and is given by $o(t) = \sum_k \delta(t - t'_k)$. The interspike intervals (ISIs) of the output train are independent because the model is reset (“leaky integration”) and the input signal is uncorrelated in time. Let us assume a time precision ε such that $\lambda\varepsilon \ll 1$. The entropy per spike of the input spike train corresponds to the entropy of a Poisson process given by $1 - \ln(\lambda\varepsilon)$. We choose a time precision of 0.1 ms. Considering that the rate of the input spike train is λ , the entropy per unit time is $H_{in} = \lambda [1 - \ln(\lambda\varepsilon)]$. Because of the independence of the output ISIs, the mutual information between the input and output spike train per unit time is given by

$$\begin{aligned} I_{io} &= I(s(t); o(t)) = I(\{t_0, \dots, t_i, \dots\}; \{t'_0, \dots, t'_k, \dots\}) \\ &= R \cdot I(\{t_0, \dots, t_i, \dots\}; T'). \end{aligned} \quad (2)$$

In the second line of the last equation the spike times are restricted to those in the interval $[t', t' + T']$,

where t' is the last output spike and the timing of the input spikes should be measured with respect to t' . In the last equation, $R = \langle T' \rangle^{-1}$ is the rate of the output spikes and $I(\{t_0, \dots, t_i, \dots\}; T') = H(T') - H(T'|_{t_0, \dots, t_i, \dots})$ is the mutual information per output spike, T' being the ISI of the output train. The entropies are $H(T') = -\int_0^\infty p(t') \ln p(t') dt'$, and $H(T'|_{t_0, \dots, t_i, \dots}) = -\langle \int_0^\infty p(t'|_{t_0, \dots, t_i, \dots}) \ln p(t'|_{t_0, \dots, t_i, \dots}) dt' \rangle_{\{t_0, \dots, t_i, \dots\}}$. An upper bound of the output entropy is given by assuming a Poisson distribution of the output ISIs with the same rate R , i.e., $p(T') = Re^{-RT'}$. This upper bound for the entropy per unit of time is therefore $H_{\max}(T') = R[1 - \ln(R\varepsilon)]$. A measure of the loss of information during the transmission is given by $L = (H_{\text{in}} - I_{\text{io}})/H_{\text{in}}$.

Let us now concentrate on the capacity of the neuron to detect two different signals. We assume (i) that there are two input spike trains, s_1 and s_2 , corresponding to different Poisson processes with rates λ_1 and λ_2 , respectively, and (ii) that the two signals are presented with uniform probability $p = 0.5$. We denote by s the random variable which corresponds to the class of the signal, i.e., the outcomes of s are s_1 and s_2 with equal probability $p = 0.5$. The task consists of discovering which signal is presented based on the analysis of the output spikes and knowing the *a priori* probability of presentation p . When one signal is presented the neuron is considered in the same initial condition corresponding to the rest potential zero. We do not consider the switching of the signal. The analysis of the output spikes is therefore performed under stationary conditions. We can measure the “discriminability” by the mutual information between s and the output spike train, i.e., by

$$\begin{aligned} I_{\text{dis}}(n) &= I(s; \{T'_1, \dots, T'_n\}) \\ &= H(T'_1, \dots, T'_n) - \langle H(T'_1, \dots, T'_n | s) \rangle_s. \end{aligned} \quad (3)$$

The entropies $H(T'_1, \dots, T'_n)$ and $\langle H(T'_1, \dots, T'_n | s) \rangle_s$ can be calculated by using the fact that, for a given input signal s_i , the output ISIs are independent. In Eq. (3) it is explicit that the discrimination task is based on the output spikes. The information about the class of the signal is of course also explicit in the statistics of the timing of the input train. However, we are more interested in studying the coding strategy of a neuron. Therefore, the explicit timing of the input spike trains is for this problem irrelevant; only its statistics, as extracted by means of the particular spiking device (neuron), is used for discovering the underlying input class. The implicit analysis performed by the neuron is reflected in the output spike statistics. In our case, for example, we classify signals which are in fact described only by the rate (Poisson signals), but we attempt to discover this rate (i.e., the name of the signal) by analyzing its influence on the output spike statistics. The maximum value of I_{dis} is given by the entropy of the random variable s , i.e., $H(s) = \ln 2$. We can study the required code, i.e., the required number of output spikes, just by analyzing the convergence of I_{dis} to the maximum value as a function of

n . The maximum value means that all of the information required for the classification is transmitted. In the case of fast convergence a small number of spikes suffice for encoding the two different signals and for discrimination of the input signals. A slower convergence means that a large amount of output spikes is required for a reliable classification of the input signals; perhaps this could also be associated with rate coding.

We integrate the diffusion and jumping processes given by Eq. (1) numerically by discretizing it in the following fashion: $V(t + \Delta t) = V(t) + (-\frac{V(t)}{\tau} + \mu)\Delta t + \sigma\sqrt{\Delta t}v + w\Delta S(t)$, where v is the standard Gaussian noise and $\Delta S(t) = \int_t^{t+\Delta t} [\sum_i \delta(t - t_i)] dt$ is the number of input spikes t_i between t and $t + \Delta t$. This Monte Carlo simulation involves the statistics of the Poisson input train and the noise. We compute the probability distribution $p(T')$ for a given resolution ε via the construction of a histogram for T' by generating new realizations of both the input train and the noise. $p(T'|_{t_0, \dots, t_i, \dots})$ is computed for a fixed realization of the input and different realizations of the noise, i.e., of the integration process. Afterwards, we change the fixed realization $\{t_0, \dots, t_i, \dots\}$ of the input spike train in order to compute the mean value $\langle \cdot \rangle_{\{t_0, \dots, t_i, \dots\}}$. In the calculation of the discriminability, the probabilities $p(T'|s_i)$ have been calculated via the construction of a histogram for T' by generating new realizations of both the input spike train for a fixed process s_i and the noise. We choose $\tau = 20$ ms and $\theta = 20$. We considered an absolute refractory time of 3 ms.

Figure 1 displays the transmitted information from input spike trains to output spike trains as a function of the

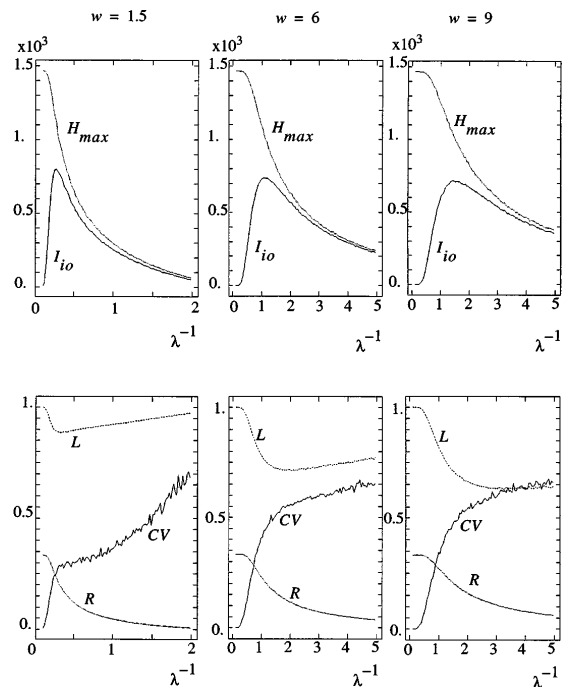


FIG. 1. H_{\max} , I_{io} , L , CV , and R for a single neuron as a function of the input mean value for three different synapses strengths.

intensity of the input signal given by its mean value. For large values of λ^{-1} the transmitted information reaches the upper bound given by the Poisson assumption. In this Poisson regime, the maximum value achievable is reached, but the efficiency of the transmission is very bad. This fact can be studied by observing the plots of the loss of information L . The minimum of information loss and therefore the maximum of efficiency is achieved *before* the Poisson regime is reached. When the synapse strength is such that the transmission is more efficient (see the deep minimum in the case of $w = 9$), the CV of the output ISIs exceeds the value 0.5 according to the experimental results of Softky and Koch [5]. This offers a possible explanation of the phenomena according to the principle of optimal information transmission. Neurons which efficiently transmit information operate in a range of parameters such that they are not in the Poisson regime but in a regime of CV of the output ISIs between 0.5 and 1.0.

Let us analyze the capabilities of a single neuron and its coding strategies in the task of distinguishing two different input signals. We study two cases. Case 1 is defined by the task of discrimination between two different input signals s_1 and s_2 presented with uniform probability and corresponding to two different Poisson processes with mean values $\lambda_1^{-1} = 2$ and $\lambda_2^{-1} = 0.11$, respectively. Case 2 considers input signals with $\lambda_1^{-1} = 1.7$ and $\lambda_2^{-1} = 1.5$. First we obtain the optimal synapse strength by maximizing numerically the efficiency estimated by the mutual information per unit time between s and 3 output spikes, i.e., $3RI_{\text{dis}}(3)$. A maximum of efficiency is obtained in $w = 9$ for case 1 and in $w = 6$ for case 2. At this optimal value of synapse strength, the output spike code should be optimal. This result is confirmed by Fig. 2. In case 1, where the separation is relatively easy, a small amount of output spikes suffices for the task of classification of the input sig-

nals. For this case, the mean output ISI is 6.20 ms when s_1 is presented and 3.33 ms for s_2 . Three output spikes are required in the optimal case for convergence to the maximum value $\ln(2)$, yielding an averaged decision time of 14.29 ms. We need three input spikes for the emission of one output spike, i.e., perfect discriminability is achieved after the analysis of about nine input spikes by the neuron. In the nonoptimal case, one spike is required but with a larger averaged decision time of 39.89 ms. In this case, the mean output ISIs are 76.75 ms by presentation of s_1 and 3.03 ms for s_2 (the big differences in the output statistics is the reason why, after one spike, we can discover which signal is presented). This result therefore theoretically confirms the possibility of classification with a timing code. In case 2 the task of discrimination is very hard. In fact, even in the optimal case, a very slow convergence of the discriminability to the maximum value is suspected. We could calculate only values of I_{dis} until $n = 3$ due to the numerical explosion in the calculation of the multidimensional integral involved in the calculation of $H(t'_1, \dots, t'_n)$. But these first three values suffice to see qualitatively that a large amount of output spikes, due to the slow convergence to the maximum, will be required for discrimination between the two input signals and that this result is probably also consistent with a rate code. The optimal w in both cases corresponds to the values where the transmission of information from input to output, i.e., I_{io} , is most efficient (see Fig. 1).

The difficulty in calculating the mutual information arises because of the presence of the term $\ln[p(x)]$ in the entropies which causes $I_{\text{dis}}(n)$ for large n to be numerically intractable. Pompe [12] introduced a generalized measure of statistical dependences that he phrased as generalized mutual information of order 2 and is given by

$$\begin{aligned} I_{\text{dis}}^{(2)}(n) &= I^{(2)}(s; \{T'_1, \dots, T'_n\}) \\ &= H^{(2)}(T'_1, \dots, T'_n) + H^{(2)}(s) \\ &\quad - H^{(2)}(T'_1, \dots, T'_n, s). \end{aligned} \quad (4)$$

In Eq. (4), the Rényi entropy of order 2 is given by $H^{(2)}(\mathbf{x}) = -\ln \int d\mathbf{x} p^2(\mathbf{x})$. When one of the variables with N outcomes is uniformly distributed, i.e., each outcome has a probability $1/N$, as in our case the variable s , the generalized mutual information $I_{\text{dis}}^{(2)}(n)$ fulfills $0 \leq I_{\text{dis}}^{(2)}(n) \leq \ln N$. Even more, the lower bound is attained if and only if the variables $\{T'_1, \dots, T'_n\}$ and s are independent, and the maximum is attained if and only if there is a function f such that $s = f(T'_1, \dots, T'_n)$, i.e., meaning an absolutely reliable classification of the input signals based in the output ISIs. For our task of classification we can use the second order generalized mutual information which allows analytical calculation and, therefore, the study of discriminability between two signals even in cases where the number of output ISIs required is large. The maximum value of I_{dis} is given again by the entropy of the random variable s , i.e., $H^{(2)}(s) = \ln 2$. In order to obtain analytical

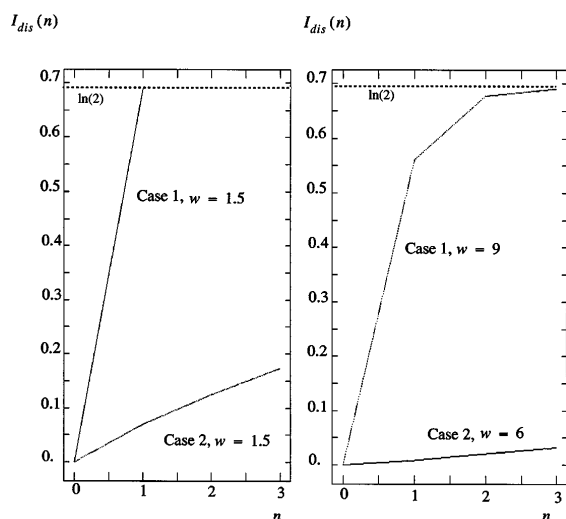


FIG. 2. Discriminability as a function of the number of output spikes considered for cases 1 and 2 and for synapses strengths nonoptimal ($w = 1.5$) and optimal ($w = 9$ for case 1 and $w = 6$ for case 2).

results we use a neural model which captures the principal effects of real neurons and which is simple enough to permit analytical calculations. The model we use is the spike response model [13]. In contrast to integrate-and-fire models which are given essentially by a differential equation, the spike response model is based on response kernels which describe the integrated effect of spike reception or emission on the membrane potential. In this model, spikes are generated by a threshold process, i.e., the firing time t' is given by the condition that the membrane potential $h(t')$ reaches the firing threshold θ , i.e., $h(t') = \theta$. The membrane potential is given by $h(t') = J \sum_i \Theta(t' - t_i) \Theta(t_i - t'_{\text{last}}) \Psi(t' - t_i)$, where $\Theta()$ is the heavyside function. We ignore the refractory time and consider a neuron with only one input spike train, which is Poisson. The response kernel used corresponds to a neuron with infinite memory, i.e., $\Psi(t' - t_i) = \Theta(t' - t_i)$. The calculation of $p(T'|s_i)$ is then reduced to the solution of the first passage time for the spike response model with an input given by a Poisson spike train. After some cumbersome algebra, we obtain $p(T'|s_i) = (\lambda_i^{m+1} T^m e^{-\lambda T'})/m!$, $m = \lfloor \theta/J \rfloor$ being the greatest integer contained in θ/J . We calculate the Rényi entropies involved in the generalized mutual information [Eq. (4)] analytically. Figure 3 shows the dependences of the generalized mutual information between the random variable s and the output spikes as a function of the number of spikes for different classification cases corresponding to input signals with $\lambda_1^{-1} = 4$ and λ_2^{-1} : (a) 40, (b) 10, (c) 7, (d) 6, and (e) 5. The maximum value of the generalized mutual information means

that the input signal can be classified with certainty, i.e., the output spikes contain the required information for a perfect and reliable distinction of the signals. In cases where the two signals to be separated are very similar, i.e., small $\Delta\lambda = \lambda_2 - \lambda_1$, the convergence of the generalized mutual information to the maximal value $\ln(2)$ is very slow, meaning that a large number of output spikes is required for a reliable classification of the signals. In contrast, in cases where the signals are very different, i.e., $\Delta\lambda$ is big, the task of classification is more simple and can be achieved with a small number of spikes.

In conclusion, the information-theoretic analysis of single central neurons which process input spike trains teaches us that (i) The maximum efficiency in the transmission of information is not reached in the Poisson regime but just before it, and in regions of high output CV. (ii) The timing code can be rigorously studied in the framework of the Rényi information concept. A small amount of output spikes suffices for efficient discrimination of input signals if the separation is easy (signals are very different); a large amount of output spikes (and probably a rate code) is required in the hard cases of separation of very similar input signals, which is consistent with the weak signal cases studied in Ref. [14]. This result is what we expect heuristically. Based on this result, we expect that an information-theoretic first principle (namely, Infomax) could be useful for defining a learning algorithm for fixing the optimal w for the task of discrimination of input signals or just for the efficient transmission of information.

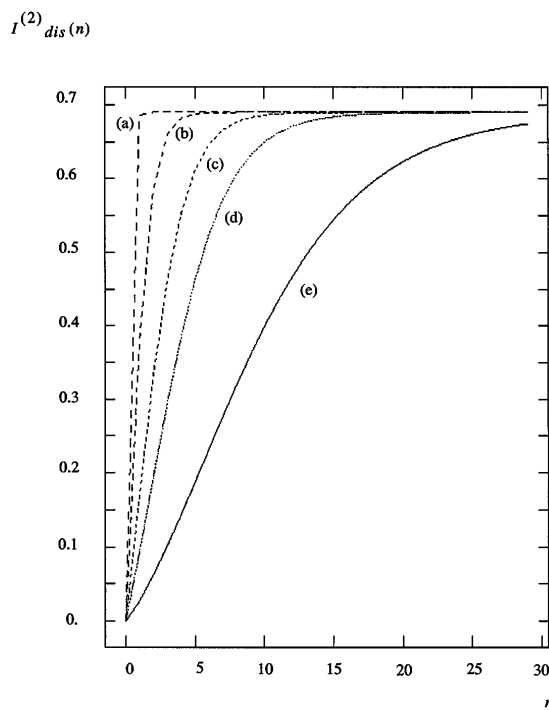


FIG. 3. Discriminability measure based on the second order Rényi mutual information as a function of the number of output spikes considered for the spike response model; see text.

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