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Information Representation and Its Application to Stochastic Resonance

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Many studies have recently focused on the temporal encoding scheme, wherein information about a stimulus is carried in temporal firing patterns of neurons. We first show how to quantify the information conveyed in the spike train of an individual neuron and that in the temporal firing patterns of an ensemble of neurons, respectively, in terms of the entropy. We further apply both the information representations to the context of stochastic resonance. It is demonstrated that the neurons can transmit more information about the signals with frequencies within the range of 22–70 Hz. These enable us to well interpret the experimental observations.

KEYWORDS: information representation, spike train, spatiotemporal firing patterns, stochastic resonance, frequency sensitivity

§1. Introduction

How single neurons or neuronal systems encode information has long been a topic of interest. It is well known that they represent input signals in sequences of discreet, identical action potentials or spikes. In the last decades, it has been assumed that a neuron's information content is contained mainly in its firing rate. Recently, much attention has centered on the temporal encoding scheme, wherein information about a stimulus is carried in precise temporal firing patterns.[1-3] Strong *et al.*[4] showed how to estimate the amount of information conveyed in this representation. In response to time dependent stimuli, the spike train of a single neuron varies, and such variability can be quantified by the entropy. The information that the spike train provides about the signal is thus characterized by the entropy (difference). Such an information measure is capable of directly demonstrating the significance of spike timing in signal encoding.

Obviously, the above information representation is concerned only with a neuron and can not be applicable to the neuronal system case. In addition, a long data sample is needed for estimation. On the other hand, more research results indicate that the brain represents the world using neural assemblies,[5,6] and that information is carried in firing patterns interpreted during a much shorter time window.[7] For example, odour identification in mammals can be possible only within 5–10 cycles of gamma frequency oscillations (30–70 Hz) in the olfactory bulb.[8] Motivated by these considerations, here we propose one approach, in terms of the entropy, to the quantification of information conveyed in firing patterns of an ensemble of neurons within a few hundred milliseconds. We further apply both the information representations to the context of stochastic resonance (SR).

SR is a cooperative phenomenon wherein the response of a nonlinear system to a weak (subthreshold) input signal is optimized by the presence of a particular level of noise (for a review see refs. 9 and 10). While SR is typically characterized by the output signal-to-noise ratio (SNR), which first rises and then drops as noise intensity increases, it is the total information encoded about the signal that is the biologically relevant quantity to consider.[11] On the other hand, although there have been many studies on SR based on the information measures, such as the mutual information (MI)[12,13] and the dynamic entropy,[14] how to quantify the information contained in spatiotemporal firing patterns has not been clearly clarified. Therefore, it is of interest to quantify the information involved in weak signal detection. In addition, we have found, in terms of the SNR, that the nervous systems are more sensitive to signals with frequencies within the range of 15–60 Hz.[15] Such frequency sensitivity is of functional significance for signal processing, which has been demonstrated experimentally.[11,16] Here we show that the neurons can transmit more information about the input signal when its frequency is within the sensitivity range, so that we can further interpret the experimental results.

§2. Model and Method

We construct a network composed of globally coupled Hindmarsh-Rose (HR) neurons, as in ref. 15. The dynamic equations for the network are presented as follows:

$$\frac{\mathrm{d}X_i}{\mathrm{d}t} = Y_i - aX_i^3 + bX_i^2 - Z_i + \sum_{j=1,j\neq i}^{N} \frac{J_{ij}}{N}\theta(X_j(t) - X^*) + I_0 + I_1\sin(2\pi f_s t) + \xi_i(t), \quad (1)$$

$$\frac{\mathrm{d}Y_i}{\mathrm{d}t} = c - dX_i^2 - Y_i, \quad (2)$$

$$\frac{\mathrm{d}Z_i}{\mathrm{d}t} = r[s(X_i - X_0) - Z_i], \quad i = 1, \dots N. \quad (3)$$

All the parameters and functions are the same as those used in ref. 15. Each neuron has a bias I_0 and is subject to a common subthreshold sinusoidal signal plus noise. In the presence of only a constant bias I_0 (<1.32), the membrane potential undergoes a damping oscillation to the resting potential from its initial state, with a frequency of 11–33 Hz.[15)] Such an oscillation is considered as intrinsic and plays an important role in signal processing. The signal amplitude I_1 is assumed to be identical for each frequency, with all the signals kept as subthreshold. Here I_0 is taken as 0.8, and I_1 is 0.11. The coupling strength J_{ij} is randomly distributed in a range, with $J_{ij} \in [-4, 20]$. $\theta(x)$ is the step function with $\theta(x) = 1$ if $x \geq 0$ and $\theta(x) = 0$ if $x < 0$. The number of neurons in the network is taken as $N = 200$. The Gaussian white noise $\xi_i(t)$ is independent of any other, satisfying

$$\langle \xi_i(t) \rangle = 0, \quad \langle \xi_i(t_1)\xi_j(t_2) \rangle = 2D\delta_{ij}\delta(t_1 - t_2), \qquad (4)$$

where D is referred to as the noise intensity.[17)] The numerical integration of eqs. (1)–(3) is done based on a second-order algorithm, and the integration step is taken as 0.01.[15)]

A firing occurs when the membrane potential $X > 0.8$;[18)] a spike train is generated in response to the stimulus. First, we quantify the information conveyed in the spike train of a neuron, closely following the method proposed in ref. 4. We discretize the spike train into time bins of width $\tau = 0.4$ ms, convert it into a sequence of "0" and "1" corresponding respectively to the nonfiring and firing states, and examine each segment in windows of length $T = 6$ ms,[19)] as shown in Fig. 1(a). Thus each possible neural response is a "word" with 15 symbols. Let $\boldsymbol{i} := i_1, \ldots i_{15}$, *e.g.*, [001000100010000], be a word. The stationary probability to observe this word shall be denoted as p_i. The entropy is thus defined in bits by

$$S = -\sum_{i=1}^{n} p_i \log_2 p_i, \qquad (5)$$

with n being the number of different words. Here at least 8000 segments lasting 48 s are analyzed to estimate the value of the entropy.[20)] The entropy is interpreted as the average information necessary to predict a word or, equivalently, as the average information gained after its actual observation. If $\{p_i\} = \{1\}$ then $S = 0$; if $\{p_i\}$ is widely distributed with a large n, S has a high magnitude. In this paper the word $[0, 0, \ldots 0, 0]$ corresponding to no firing always takes the largest probability P_{max}. We also compute the noise entropy $\tilde{N}$, which measures the variability of the spike train to repeated presentations of the same stimulus. Thus the difference between both entropies, $R_{inf} = S - \tilde{N}$, characterizes the information that the spike train conveys about the stimulus.

However, the above representation can not quantify the information transmitted by the network. To this end we record the firing patterns of all neurons by plotting the firing time versus the neuron index, and discretize them into time bins (with the same τ). Thus a word consists of 200 symbols ("0" or "1") corresponding to the firing state of the network, as depicted in Fig. 1(b). The new entropy is similarly defined as

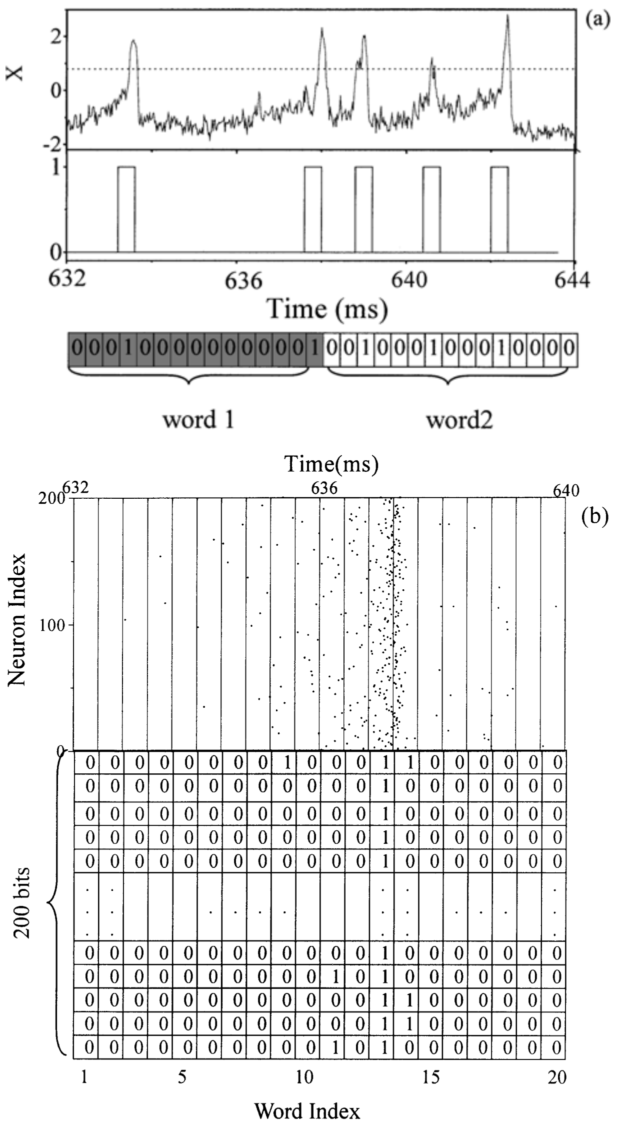

Fig. 1. Schematic of the calculation of the entropy correlated (a) with the spike train of a neuron and (b) with the temporal firing patterns of neurons.

$$S^* = -\sum_{j=1}^{n^*} p_j^* \log_2 p_j^*, \qquad (6)$$

with p_j^* denoting the normalized count of the jth word and n^* the number of different words. To estimate the magnitude of S^*, we analyze the data window with 750 words lasting 300 ms, which is nearly consistent with the duration of typical neural responses. It is noted that S^* is closely correlated with the spatiotemporal firing patterns. If the system exhibits a strong synchronization, S^* instead has a small value. The information conveyed in the spatiotemporal firing patterns is determined by $R_{inf}^* = |\tilde{N}^* - S^*|$ with $\tilde{N}^*$ being the corresponding noise entropy.

§3. Results and Discussion

We can calculate the information involved in weak signal detection based on the aforementioned information representations. Figure 2 shows the information carried in an individual neuron within the network, R_{inf}, versus

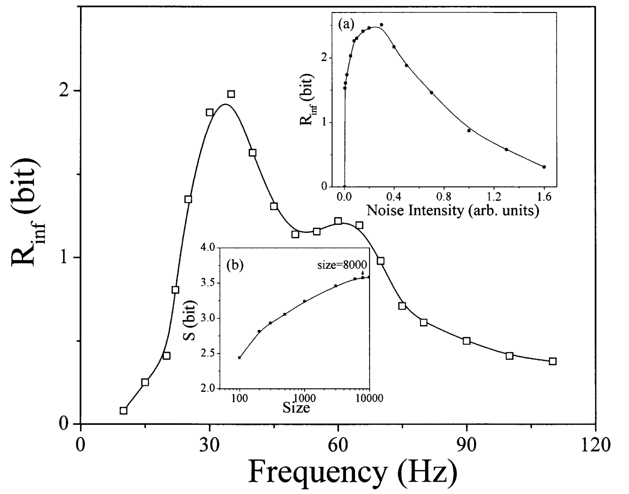

Fig. 2. R_{inf} vs the signal frequency in the case of $D = 0.5$ for the 1st element within the network. The inset (a) is R_{inf} vs the noise intensity in the case of $f_s = 30\,\text{Hz}$ and (b) is the entropy S vs the data size in the case of $f_s = 30\,\text{Hz}$ and $D = 0.5$.

the signal frequency in the case of $D = 0.5$. Clearly, R_{inf} has a relatively large value around $f_s = 30\,\text{Hz}$, indicating that the neuron can transmit more information about signals with frequencies in the range of 22–70 Hz. That is, the neuron is more sensitive to these signals. This is nearly consistent with the results obtained in ref. 15. Physically, such frequency sensitivity results from the resonance between the intrinsic oscillation of the neuron and the input signal. In fact, the intrinsic oscillation frequency corresponding to $I_0 = 0.8$ is just $f = 30\,\text{Hz}$. In the presence of the signal with $f_s = 30\,\text{Hz}$, the neuron is easily evoked to fire and always discharges spikes around the maxima of the signal, exhibiting a coherence with the input. Therefore, P_{max} takes the smallest value (~0.67) and n is the largest, as the neuron may fire one spike or in bursts near the maxima of the signal. As a result, S has the largest value, and the neuron can transfer more information about the signal. In response to the signal with a lower frequency, although the neuron can fire every period, the firing is random and is not phase locked to the signal. When subject to the signal with a higher frequency, the firing of the neuron is often interrupted during several driving cycles since the neuron needs more spatiotemporal summations to fire. In both the latter cases, P_{max} has a larger value and n takes a smaller value, resulting in a small R_{inf}. It is noted that there exists a local maximum around $f_s = 60\,\text{Hz}$, due to the resonance between the signal and the second-order harmonic of the intrinsic oscillation.

The inset (a) of Fig. 2 shows R_{inf} versus the noise intensity D in the case of $f_s = 30\,\text{Hz}$. Apparently, there appears a maximum around $D = 0.3$, suggesting that a nonzero level of noise can evoke the neuron to convey more information about the signal, which is just the reflection of the SR effect. This can be understood as follows. Both S and $\tilde{N}$ rise as D increases. Once a very low noise is applied, say $D = 0.01$, the neuron can be evoked to fire, and R_{inf} rises rapidly from zero. In the case of low noise, the firing is often separated by several driving cycles, leading to a small R_{inf}. At a moderate noise level, the neuron always discharges around the maximal of the signal, and thus R_{inf} rises and reaches its maximum. As D further rises, the neuron fires more frequently, and the firing coherence with the input degrades. Thus R_{inf} drops gradually. Therefore, the information representation can characterize both the effects of SR and the frequency sensitivity. It is noted that the magnitude of the entropy depends on the data size (i.e., the number of segments). The inset (b) of Fig. 2 depicts how S converges as the size of data set increases. This also indicates that our estimation of the entropy is a good approximation to the true one.

Now we turn to investigate the information carried in the firing patterns of neurons. Figure 3(a) shows R^*_{inf} versus D for the signals with frequencies of $f_s = 10$, 30, and 100 Hz, respectively. In the case of very low noise, owing to small effective stimulus strength, the neurons rarely fire, and $\tilde{N}^*$ has a small value with $\tilde{N}^* < S^*$. As D rises, both S^* and $\tilde{N}^*$ increase, but there exists a 'critical' $D_c \sim 0.12$, where $\tilde{N}^*$ is larger than S^*. Thus there exists a minimum at a low noise level. In addition, there appears a maximum around $D = 0.4$. This can be understood as follows. In the case of low noise, the firings of neurons are often interrupted within several driving cycles. As D rises, the firing rate increases, and

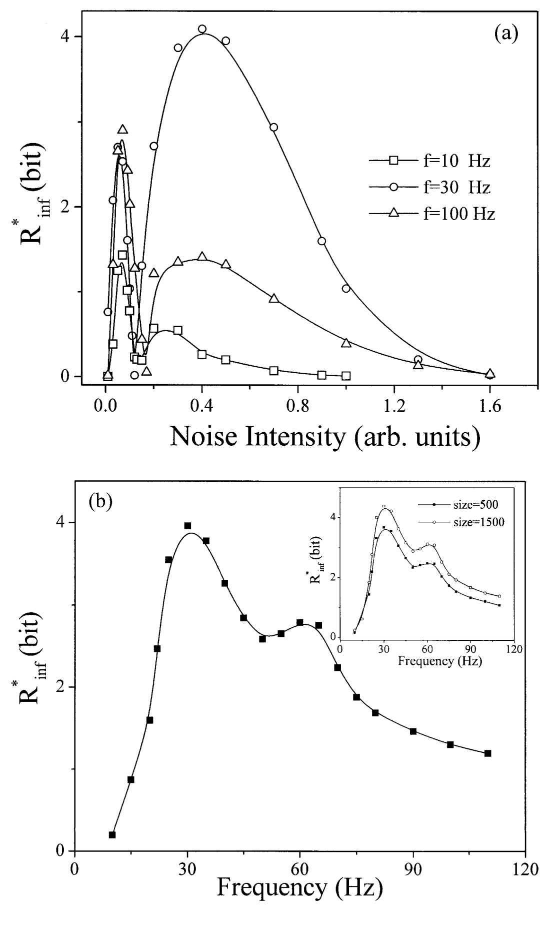

Fig. 3. (a) R^*_{inf} vs the noise intensity for the signals with $f_s = 10$ (□), 30 (○), and 100 Hz (▽), respectively. (b) R^*_{inf} vs the signal frequency in the case of $D = 0.5$ with 750 and 500 as well as 1500 (in the inset) words analyzed, respectively.

the neurons can fire synchronously although there exits a marked time lag relative to the maxima of the signal. Thus there can exist a local maximum in R^*_{inf} around $D = 0.05$. After that, due to more effective stimulus strength, the firing time becomes somewhat scattered, and this results in the drop of R^*_{inf}. If $D > D_c$ the neurons nearly fire every period; as D rises, the firings occur closer to the maxima of the signal in each period. When the neurons fire synchronously around the maxima of the signal, R^*_{inf} reaches its maximum. If D further increases, the neurons fire more frequently, and the synchronization becomes weak, resulting in the drop of R^*_{inf}. Thus R^*_{inf} is closely related to the firing correlation between the neurons. Such an information measure also demonstrates that the response of the system to the signal can be optimized by a nonzero level of noise. If we pay attention only to $D > D_c$, R^*_{inf} for the case of $f_s = 30\,\text{Hz}$ always has a larger value than that for $f_s = 10$ and $100\,\text{Hz}$, respectively, implying that the network transmits more information about the signal with $f_s = 30\,\text{Hz}$.

Figure 3(b) shows R^*_{inf} versus the signal frequency in the case of $D = 0.5$. Clearly, there exist maxima around $f_s = 30$ and $60\,\text{Hz}$, respectively, and R^*_{inf} has a large value for signals with frequencies within the range of 22–70 Hz. The result verifies that the neuronal system is more sensitive to these signals, conveying more information about them. This is quite in agreement with the results of Fig. 2. In addition, when the data window has a different size, similar features to the above can be observed, as seen in the set of Fig. 3(b), which presents R^*_{inf} in the cases of 500 and 1500 words, respectively. The difference between R^*_{inf} becomes much smaller as the data size rises. In fact, for the estimation of R^*_{inf} we need only a short data window, which is consistent with the duration of typical neural response (hundreds of milliseconds). In contrast, a much longer data sample is needed to compute R_{inf}. Thus it is possible that the neurons can process transient signals in parallel. In a sense, the information characterization for the network case is of more biological significance.

Just as mentioned above, the amount of the information conveyed in the temporal firing patterns is closely associated with the extent to which the network exhibits the spatiotemporal synchronization. This can be clearly seen in Fig. 4. Figure 4 shows the spatiotemporal firing patterns for $f_s = 10$, 30, and $100\,\text{Hz}$, respectively, in the case of $D = 0.5$. Obviously, the network exhibits a strong spatiotemporal synchronization for the case of $f_s = 30\,\text{Hz}$. The neurons fire spikes around the maxima of the signal, showing a coherence with the input due to the resonance between the intrinsic oscillation and the input signal. The probability P^*_{max} for the word $[0, 0, \dots 0, 0]$ takes the largest value ($\sim$0.5). S^* has the smallest value and is much smaller than $\tilde{N}^*$, resulting in the largest value of R^*_{inf}. In the cases of $f_s = 10$ and $100\,\text{Hz}$, the network exhibits a weak synchronization. P^*_{max} takes a much smaller value, and n^* has a large value, leading to a large S^*. In sum, the network transmits more information if the neurons fire synchronously.

Now we can make a comprehensive interpretation of

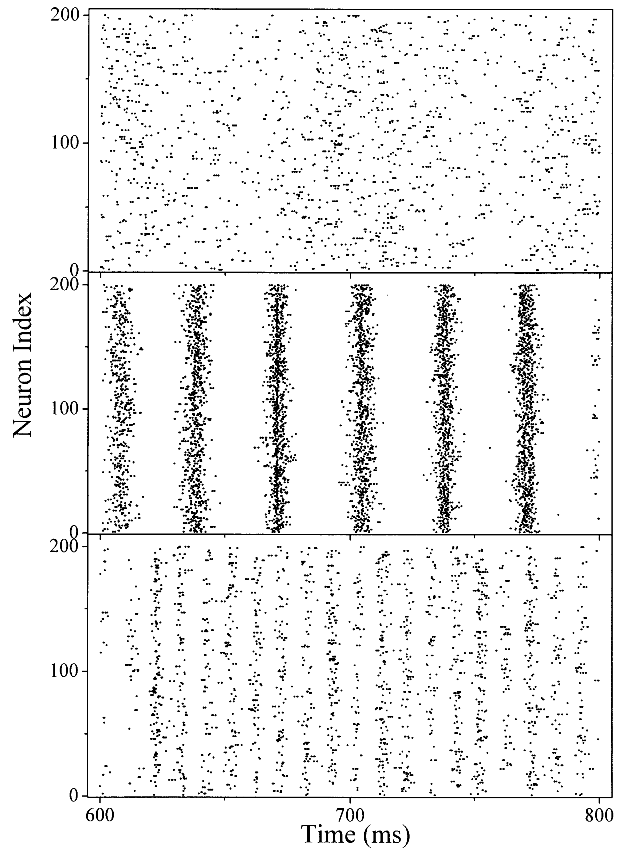

Fig. 4. The spatiotemporal firing patterns are plotted by recording the firing time t^i_n, defined by $X_i(t^i_n) > 0.8$ and $X_i(t^{i-}_n) < 0.8$, vs the neuron index for $f_s = 10$, 30, and 100 Hz (from top to bottom), respectively, in the case of $D = 0.5$.

the effect of frequency sensitivity based on both the SNR and the information measures. Both indicate that the neural systems are more sensitive to weak signals with frequencies within the gamma frequency band, owing to the resonance between the intrinsic oscillation of the system and the input signal. In particular, the information measures directly exhibit that the neurons can transmit more information about these signals. Such frequency sensitivity is of much interest. On one hand, it has been widely reported that there exist large-scale synchronous oscillations in the same frequency band (see ref. 21 and references therein); on the other hand, our results indicate that the input signals with such frequencies can evoke the neurons to convey more information about them. Thus it is possible that the nervous systems may combine both to represent the world. Compared with the SNR measure, the information measure has a wide applicability. For example, if the input signal is aperiodic, the SNR measure is not well defined, whereas the information measure provides a useful tool. In addition, although both the information representations can demonstrate the effects of SR and the frequency sensitivity, R^*_{inf} is closely associated with the spatiotemporal encoding scheme and acquires only a short sequence of data, whereas to calculate R_{inf} needs a long data set. The results also imply that population coding may be more subtle in signal processing, and help us understand why the neural assemblies can fulfill their functions within a few hundred milliseconds.

In conclusion, we have quantified the information carried both in the spike train of an individual neuron and in the spatiotemporal firing patterns. The information representations can characterize both the effects of SR and the frequency sensitivity. It is shown that the neurons can transmit more information about the signals with frequencies in the range of 22–70 Hz. In particular, the information representation correlated with the spatiotemporal encoding scheme can provide an efficient approach to the estimation of information flow in a complex system, such as the nervous system.

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17) For the HR neuron, the time scale is defined as ten units of eqs. (1)–(3) equaling 2 ms, which is the width of the action potential in the absence of noise. In the presence of noise, the firing threshold is taken as a larger value (0.8) to eliminate the false spikes, and the width of the spike becomes short, defined as 0.4 ms (2 units). Here the value of D is defined based on the time scale of eqs. (1)–(3). If the time is in units of seconds, the value of noise intensity is taken as $D' = 2 \times 10^{-4} D$.
18) It is noted that a firing is followed by an absolute refractory period (0.1 ms) wherein no positive-going threshold crossing is considered as a spike.
19) For large T, very large data sets are required to ensure the convergence of the entropy. In addition, to study the responses of the neuron to the periodic signal with a frequency between 10 and 120 Hz, it is desired that each period includes at least a word since the firing dynamics is modulated by the signal. Thus an intermediate value is chosen for T.
20) In fact, as discussed in ref. 4, the true entropy should be the extrapolated value to the infinite data limit. Our simulations have demonstrated the convergence of the entropy in the case of a large data size.
21) For example, W. Wang, G. Chen and Z. D. Wang: Phys. Rev. E **56** (1997) 3728.