Frequency Sensitivity in Nervous Systems *

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We first demonstrate how to quantify the information conveyed in temporal firing patterns of neurons. We then show that neurons are more sensitive to signals with frequencies within the range of $20 - 70$ Hz in weak signal detection. Such frequency sensitivity is characterized by both the output signal-to-noise ratio and the information measures.

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Recently, stochastic resonance (SR) has been intensively studied in a large variety of nonlinear systems, especially in the nervous system.[1] It was demonstrated that noise can play a constructive role in signal processing. Particularly, it was found experimentally that there exists a frequency sensitivity range of $5 - 60$ Hz, within which the response of neurons to the signal is significantly enhanced.[2] A theoretical interpretation has also been proposed.[3]

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.[2] There have been many studies on how neurons encode information about the stimuli, and much attention has recently centred on the temporal encoding scheme, wherein information about a stimulus is carried in precise temporal firing patterns of neurons.[4] Here we first demonstrate how to quantify the information conveyed in this representation and then show, in terms of both the SNR and the information measures, that the neurons are more sensitive to signals with frequencies within a range of $20 - 70$ Hz.

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

$$
\begin{aligned}
\frac{dX_i}{dt} &= Y_i - aX_i^3 + bX_i^2 - Z_i \\
&\quad + \sum_{j=1, j\neq i}^{N} \frac{J_{ij}}{N}\theta(X_j(t) - X^*) + I_0 \\
&\quad + I_1 \sin(2\pi f_s t) + \xi_i(t), \qquad (1) \\
\frac{dY_i}{dt} &= c - d\,X_i^2 - Y_i, \qquad (2) \\
\frac{dZ_i}{dt} &= r\,[\,s\,(X_i - X_0) - Z_i\,], \qquad i = 1, \cdots N. \quad (3)
\end{aligned}
$$

All the parameters are the same as those used in Ref. 3. Each neuron has a bias I_0 and is subject to a common subthreshold sinusoidal signal plus noise. In the pres-

ence 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.[5] 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 $J_{ij} \in [-4, 20]$, and $\theta(x)$ is the step function. The number of neurons in the network is taken as $N = 200$. The Gaussian white noise $\xi_i(t)$ is independent of any other noise, satisfying

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

where D is referred to as the noise intensity. For the HR neuron, the timescale is defined as ten units of Eqs. (1)−(3) equaling 2 ms. Here the value of D is defined based on the timescale of Eqs. (1)−(3). If the time is in units of seconds, the value of noise intensity is taken as $D' = 2 \times 10^{-4}D$. The integration step is taken as 0.01, and an average over 50 different noise realizations is always taken.

A spike occurs when the membrane potential $X > X^* = 0.8$. The firings of each neuron are recorded and converted into a time series of standard pulses $V_i(t)$ with $V_H = 1$ of width 0.4 ms and $V_L = 0$ corresponding to firing and non-firing states, respectively. The output of the network is defined as

$$
I^{\mathrm{out}}(t) = \frac{1}{N}\sum_{i=1}^{N} V_i(t). \qquad (5)
$$

This is different from that in Ref. 3, where $I^{\mathrm{out}}(t)$ is defined as $(1/N)\sum_{i=1}^{N}\theta(X_i(t) - X^*)$. Here the value of the SNR becomes large after we convert the spike train into a series of standard pulses.

The SNR is defined as $10\log(\Gamma/B)$ with Γ and B representing the signal strength and the mean amplitude of the background noise at the input signal frequency in the power spectrum, respectively. Here we

always take the output of the first neuron, denoted as $U(t)$, as the representative for the individual responses within the network. The SNR for $I^{\mathrm{out}}(t)$ and $U(t)$ is simply denoted as γ_{o} and γ_{u}, respectively.
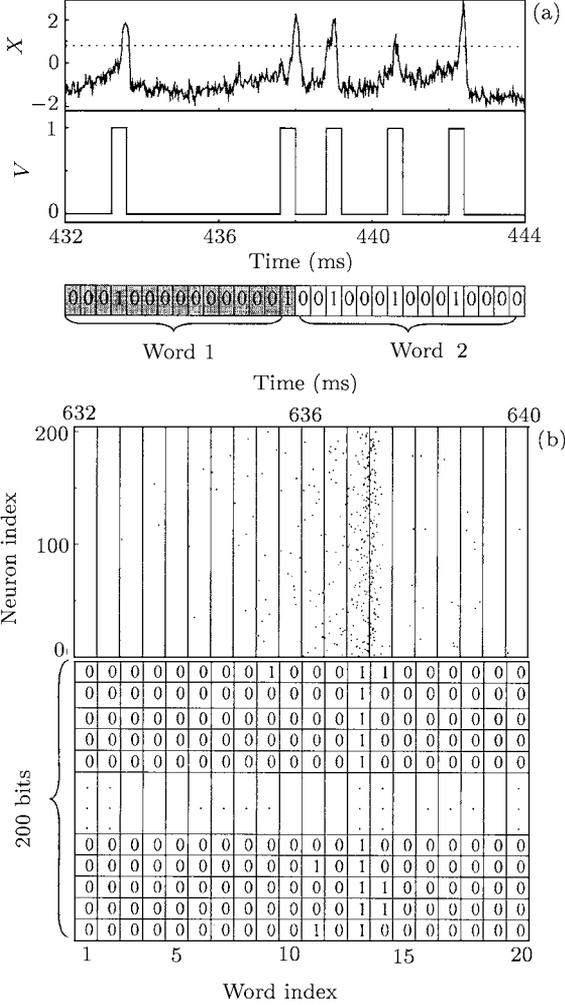

Fig. 1. A schematic diagram of the calculation of entropy correlated (a) with the spike train of a neuron and (b) with the temporal firing patterns of neurons.

In response to time-dependent stimuli, the spike train of a neuron varies, and such variability can be characterized by the entropy. The information that the spike train conveys about the signal is thus quantified by the entropy (difference). We first specify the information conveyed in the spike train of a neuron, closely following the method proposed in Ref. 6. Just as stated above, we discretize the spike train into a sequence of "0" and "1", and examine each segment in windows of length $T = 6$ ms, as shown in Fig. 1(a). It is noted that for large T very large data sets are required to ensure the convergence of the entropy. On the other hand, in the presence of a periodic signal, it is desirable that each period includes at least a word since the firing dynamics is modulated by the signal. As a result, an intermediate value is chosen for T. Thus each possible neural response is a "word" with

15 symbols. Let $i = i_1, \cdots i_{15}$, say [01000010000100], be a word. The stationary probability to observe this word shall be denoted as p_i. Thus the entropy is defined in bits by

$$S = -\sum_{i=1}^{n} p_i \log_2 p_i, \qquad (6)$$

with n being the number of different words. In this letter, the word $[0,0,\cdots 0,0]$ corresponding to no firing always takes the largest probability. Here at least 8000 segments lasting 48 s are analysed to estimate the value of the entropy. We also compute the noise entropy $\tilde{N}$, which measures the variability of the spike train to repeated presentations of the same stimulus, so that the difference between both entropies, $R_{\mathrm{inf}} = S - \tilde{N}$, characterizes the information that the spike train conveys about the stimulus. In sum, we need two different entropies to specify the information: S quantifies the variations across time and sets the capacity of the spike train to carry information, while $\tilde{N}$ measures the irreproducibility from trial to trial.

However, the above representation cannot quantify the information transmitted by the network. We propose the following approach. We record the firing patterns of all neurons by plotting the firing time versus the neuron index, and discretize them into time bins of the same width $\tau = 0.4$ ms. 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

$$S^* = -\sum_{j=1}^{n^*} p_j^* \log_2 p_j^*, \qquad (7)$$

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 analyse 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. The information conveyed in the temporal firing patterns of neurons is determined by $R_{\mathrm{inf}}^* = \mid \tilde{N}^* - S^* \mid$ with $\tilde{N}^*$ being the corresponding noise entropy.

Figure 2(a) shows both γ_{o} and γ_{u} versus the noise intensity D. The curves exhibit the typical characteristic of SR: first a rise and then a drop. The physical argument for this was clearly presented in Ref. 3. We note that, according to the definition of $I^{\mathrm{out}}(t)$, the averaging of the firings of all neurons strengthens the periodic feature of the output of the network and averages out the random feature of firings of the individual neurons. Therefore, γ_{o} has a much larger value than γ_{u}, and this also indicates that the coupling can enhance signal processing.
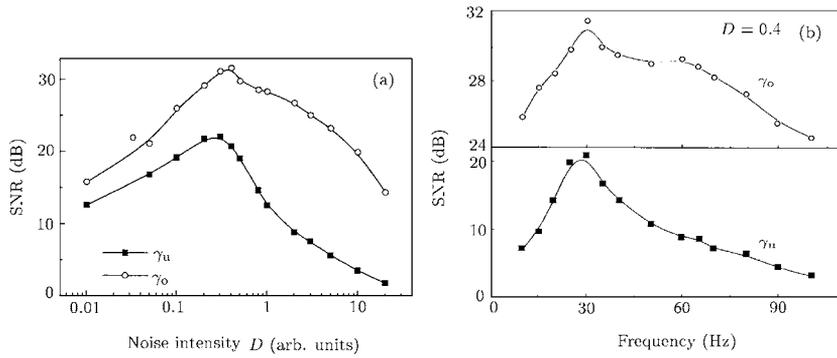
Fig. 2. (a) Behaviour of γ_o and γ_u versus the noise intensity for the case of $f_s = 30$ Hz. (b) γ_o and γ_u versus the signal frequency.

Fig. 3. Amount of information conveyed in the spike train of the first neuron within the network and that in the temporal firing pattern versus the signal frequency.

Figure 2(b) shows γ_o and γ_u versus signal frequency in the case of $D = 0.4$. Clearly, the SNR has a relatively large value for signals with frequencies within the range of $20 - 70$ Hz, which is more apparent in the curve of γ_o. That is, the neurons are more sensitive to those signals. Physically, such frequency sensitivity results from the resonance between the intrinsic oscillation of the neurons and the input signal. In fact, the intrinsic oscillation frequency corresponding to $I_0 = 0.8$ is just $f = 30$ Hz. In the presence of the signal with $f_s = 30$ Hz, the neurons are easily evoked to fire and always discharge spikes near the maxima of the signal, exhibiting a coherence with the input. In response to the signal with a lower frequency, although the neurons can fire every period, the firings are random and are not phase locked to the signal. When subjected to the signal with a high frequency, the firings of the neurons are often interrupted during several driving cycles since the neurons need more spatiotemporal summations to fire. In both the latter cases, the SNR has a small value. It can be seen that there exists a local maximum in γ_o around $f = 60$ Hz, due to the resonance between the signal and the second-order harmonic of the intrinsic oscillation.

Now we turn to investigate the information involved in weak signal detection. Fig. 3 shows the information contained in the spike train of the individual neurons and that in the spatiotemporal firing patterns, respectively, versus the signal frequency in the case of $D = 0.4$. Obviously, in both curves there exist maxima around $f = 30$ and 65 Hz, respectively, while both R_{inf}^* and R_{inf} are large for signals with frequencies within the range of $20 - 70$ 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(b). In fact, the amount of information conveyed in the spatiotemporal firing pattern is closely related to the spatiotemporal synchronization. The network exhibits a strong spatiotemporal synchronization in the case of $f_s = 30$ Hz, while the neurons present weak relevance
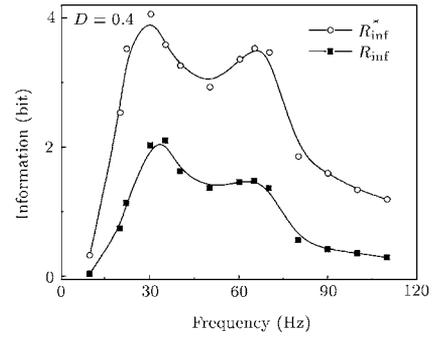
in firing for the cases of $f_s = 10$ and 100 Hz. In addition, although here we analyse a short data window for the estimation of R_{inf}^*, the results are basically the same for a longer data sample. Thus it is possible that the neurons extract the information from transient signals by processing in parallel. This may also help us understand why nervous systems can perform functions within hundreds of milliseconds. It is worth noting that such frequency sensitivity in weak signal detection can also be observed in different information representations. The details will be presented elsewhere.

We can make a comprehensive interpretation on the effect of frequency sensitivity in weak signal detection based on both the SNR and the information measures. Both indicate that the neural systems are more sensitive to weak signals with frequencies within nearly the same frequency band as reported in Ref. 2, 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 those signals. Such frequency sensitivity is of much interest. On the one hand, it has been widely reported that there exist large-scale synchronous oscillations in the same frequency band (see Ref. 7 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 advantageous that the nervous systems may combine both to represent the world.

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