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Spike timing precision for a neuronal array with periodic signal

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Abstract

The spike timing precisions of an array of neurons to periodic input are studied. For weak signal, the precision versus the noise intensity shows a stochastic resonance (SR) behavior. The optimal noise intensity corresponding to the maximal resonance shows a global minimum as increasing signal frequency. As the signal amplitude increases above a critical value, the SR effect disappears, and the critical amplitude goes through a global minimum as the signal frequency increases. A frequency sensitive range of 30–100 Hz with high spike timing precisions and high coherence of the firings are found. It is the resonance between the intrinsic oscillation and the signal resulting in the dependence of the dynamical features of SR on the forcing frequency and the frequency sensitivity. © 2001 Elsevier Science B.V. All rights reserved.

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A number of recent experimental and theoretical studies on the information processing in neuronal systems demonstrated the role of the precise spike timing in the information encoding and transmission [1–5], leading to a temporal coding. Using temporal coding the information capacity of neural spike trains increases significantly [1–5]. A common feature of the temporal coding is the synchronization of spikes among the population of the neurons. The precision of the spike timing is used to characterize the coincidence, so the synchronization, of the spike firings among the neurons. It is argued that the synchronized activities of the neurons with high temporal precision can be transmitted more efficiently than the asynchronous ones [2,3]. Thus, the degree of precision of

the spike timing determines whether subsequent neuronal groups can reproduce (or improve) the activities, i.e., whether the precise spikes can propagate stably among the neuronal groups or whether it dies out in the process of propagation. Besides, the influence of noise on the spike timing precision of neural signals has attracted much attention. A study by Pei et al. [5] showed that spike timing precision of the neurons to an aperiodic subthreshold stimuli can be effectively enhanced by a suitable noise via a so-called mechanism of the stochastic resonance (SR) [6].

It is well known that in peripheral or central nervous system the information processing is generally accompanied by some rhythmic oscillations of neural activities. These rhythmic oscillations, definitely related to the intrinsic oscillations of the neurons, are ubiquitous phenomena [7,8]. Furthermore, both experimental and theoretical studies [3,9] indicated that these oscillations may serve as functional synchronizing and tim-

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ing devices for information processing. Moreover, a phenomenon of frequency sensitivity in weak signal detection has been examined experimentally [10] and theoretically [11], respectively. It was found that there exists a frequency range of 30–100 Hz in which the signal detection or transduction of the neuron is more effective [10,11]. That is, in this range the coherence of the spiking responses of the neurons to the input signal is evidently enhanced, improving its ability in information processing. It is suggested that such a frequency sensitivity is a result of a resonance between the intrinsic oscillation of the neuron and the input signal [10,11]. It is interesting to examine how this intrinsic oscillation influences the spike timing precision in response to weak periodic stimuli and the dynamical behavior of SR. Do the neural systems favor some signals with specific frequencies in information processing?

To address the mentioned above questions, we make a study on the pooling effect of the responses of a large number of noisy Hodgkin–Huxley (HH) neurons [12] in parallel as such an array architecture may be involved in sensory systems [2,13]. The input signal is selected as a periodic one because of its biological relevance [13,14]. The spike timing precision of the neurons in the array to the subthreshold periodic signal is found to be maximized by the optimal noise intensity D_{opt} via SR. The D_{opt} corresponding to the maximal resonance shows a global minimum as increasing the signal frequency. The critical amplitude of signal above which the SR effect disappears is obtained, which also goes through a global minimum as increasing the signal frequency. By matching the period of stimulus to that of the intrinsic oscillation of the neurons, the spike timing precision of the neurons for the signal is largely enhanced, especially when the frequency of the signal is in a range of 30–100 Hz. The characterization of such a resonance and the frequency preference capture some essential properties of neurons that may serve as a substrate for coordinating network activities around a frequency range of the so-called γ -band (40 Hz) in the brain.

We report here the results of a numerical simulation of a summing network of 1000 HH neurons connected in parallel and converging on a summing center Σ , as shown in Fig. 1. The HH neuronal model is an useful paradigm that accounts naturally for both the spiking behavior and refractory properties of real

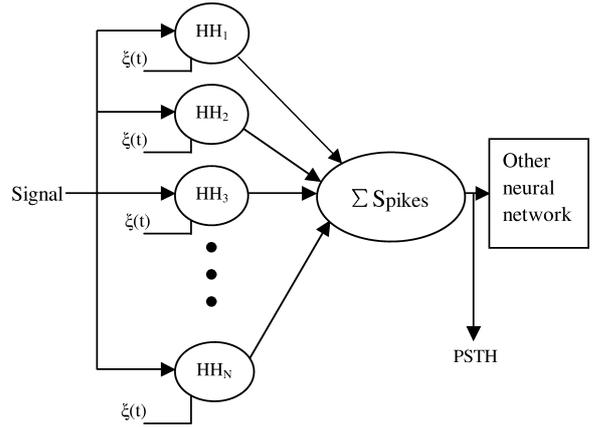


Fig. 1. A schematic diagram of the parallel array of HH neuron models convergent on a summing center Σ . The sum of the output of the array may be assumed as an input to other neural network.

neurons [12]. The dynamic equations for the network are presented as follows:

$$C_m \frac{dV_i}{dt} = I_{\text{ext}}(t) - g_{\text{Na}} m_i^3 h_i (V_i - V_{\text{Na}}) - g_{\text{K}} n_i^4 (V_i - V_{\text{K}}) - g_{\text{l}} (V_i - V_{\text{l}}) + \xi_i(t), \quad (1)$$

$$\frac{dm_i}{dt} = \frac{m_{\infty}(V_i) - m_i}{\tau_m(V_i)}, \quad (2)$$

$$\frac{dh_i}{dt} = \frac{h_{\infty}(V_i) - h_i}{\tau_h(V_i)}, \quad (3)$$

$$\frac{dn_i}{dt} = \frac{n_{\infty}(V_i) - n_i}{\tau_n(V_i)}, \quad i = 1, \dots, 1000, \quad (4)$$

where V_i , m_i , h_i and n_i are the membrane potential, the gating variables of Na^+ and K^+ channels, respectively. g_{Na} , g_{K} and g_{l} are the maximal values of conductance of the sodium, potassium, and leakage currents; and V_{Na} , V_{K} and V_{l} are the corresponding reversal potentials. The membrane capacity $C_m = 1 \mu\text{F}/\text{cm}^2$. The auxiliary functions and the parameter values can be found in Ref. [12]. $I_{\text{ext}}(t) = I_1 \times \sin(2\pi f_s t)$ is an input signal with I_1 and f_s being the amplitude and frequency, respectively.

It is well known that there are numerous noise sources in nervous systems [15], such as thermal fluctuations, the variability of membrane parameters, and spontaneous opening or closing of ion channels, which can be modeled as a Gaussian white noise $\xi(t)$

with zero mean and autocorrelation as follows:

$$\begin{aligned} \langle \xi_i(t) \rangle &= 0, \\ \langle \xi_i(t_1)\xi_j(t_2) \rangle &= 2D\delta_{ij}\delta(t_1 - t_2), \end{aligned} \quad (5)$$

where $\langle \dots \rangle$ represents the ensemble average over the noise distributions. Each neuron within the array is subjected to an independent Gaussian white noise but with the same intensity D . All the numerical simulations are done by using a stochastic Runge–Kutta algorithms [16] to obtain more precise solution. The integration step is taken as 0.02 ms.

The dynamic features of a noisy HH neuron has been studied in detail in many works (for example, see Refs. [17–19]). The weak noise makes the membrane potential fluctuate near the firing threshold and display sustaining subthreshold oscillations. Such oscillations are mainly around frequencies about 50–60 Hz [19]. When the noise intensity increases slightly large, coherent oscillations (firings around a main frequency) occur which may relate to a coherence resonance (CR) [20]. As reported in Refs. [18,21], the coherent motion of the neuron is maximized by a noise with optimal intensity. Each coherent oscillation possesses a definite frequency which might be associated with the natural frequency of the neuron [18,21]. For the HH neurons, the frequencies of coherent oscillations for various noise intensities are mainly within 40–70 Hz [19]. Both subthreshold oscillations and coherent oscillations can be induced by noise, and these oscillations can be viewed as intrinsic oscillations of the HH neurons. Actually, these oscillations have also been observed in experiments in various neuron types, such as in the neocortical neurons [7] and in the thalamic neurons as well [8]. Physically, the intrinsic stochastic nature of the neuron, and the inherent bistability of the neuron play important roles in generating these subthreshold and coherent oscillations [17–19].

Recently, these oscillations were suggested to provide a precise temporal clock for neurons in the information encoding and even supply a mechanism underlying synchronizing and binding functions for the neuronal activities [3,10]. It was also suggested that the nature frequency exhibits in these oscillations may provide the neural systems an effect of frequency preference to synaptic inputs, which results in a phenomenon of frequency sensitivity in processing input signals [10,17,19].

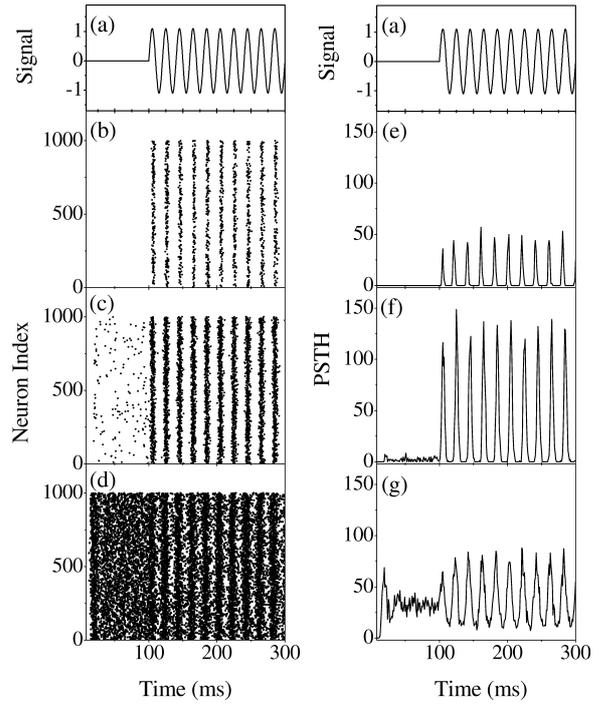


Fig. 2. (a) An example subthreshold signal with frequency $f_s = 50$ Hz and $I_1 = 1 \mu\text{A}/\text{cm}^2$. (b)–(d) Raster plot of spike times of the network for the stimulus in (a): for small noise $D = 0.1$ (b), mediate noise $D = 1$ (c), and large noise $D = 10$ (d). (e)–(g) The PSTHs resulting from the stimulus in (a): for small noise $D = 0.1$ (e), mediate noise $D = 1$ (f), and large noise $D = 10$ (g).

We input a weak periodic signal $I_1 \sin(2\pi f_s t)$ with $I_1 = 1 \mu\text{A}/\text{cm}^2$ and $f_s = 50$ Hz to each noisy neurons in the array and examine the effect of the noise and the intrinsic oscillations on the firing precision of the neurons. Figs. 2(a)–(d) show the input signal and the resulting firing spatiotemporal patterns for three noise intensities. Before the onset of the stimulus, all the firings are disordered in time due to the noise. When the stimulus is added, synchronized firings are achieved because the periodic signal represents an external time clock in adjusting the firing phase of each neuron. The corresponding post stimulus time histograms (PSTH), which shows the number of spikes collected at the output of the summing center per unit time, are shown in Figs. 2(e)–(g), respectively. The PSTH as a function of time is known as the instantaneous firing rate. It was assumed that this function encodes the information of the signal [1,4]. But we should realize the artificial nature of this construct. Many recent theoretical works

have emphasized the idea that the spike coincidence across a group of neurons, as represented by the array in Fig. 1, encodes the information, which may be neglected in rate coding. The correlation of the temporal spike timing among different groups of neurons may represent an important signal for a number of perceptual processes [4]. In order to quantify the coincidence of the spike timing of a group or an array, we define the spike timing precision p_j for j th firing event (the j th peak, consists of a number of spikes) in the PSTH, based on the shape of a smoothed data set obtained as a five point moving average of the PSTH [5],

$$p_j = (\text{PSTH})_{\max}^j / W_j, \quad (6)$$

where $(\text{PSTH})_{\max}^j$ is the maximum value of the height of the j th firing event in the PSTH, and W_j is the width at the height $(\text{PSTH})_{\max}^j / e$ (e is the base of natural logarithms). Thus, for one periodic signal, the average precision p is obtained by averaging over all firing events M during the full stimulus process, i.e.,

$$p = \frac{1}{M} \sum_{j=1}^M p_j, \quad j = 1, \dots, M. \quad (7)$$

p describes quantitatively the average number of spikes and the coincidence of these spikes in any firing event in the PSTH.

Intuitively, the PSTHs in Fig. 2 shows that the spike timing precision for intermediate noise intensities, e.g., $D = 1$, is larger than those for a small (e.g., $D = 0.1$) and a large noise intensities (e.g., $D = 10$), respectively. This means that there is an optimal noise intensity for a maximal precision, relating to a SR-like behavior, which is similar to the observation by Pei et al. [5]. (Differently, the input Pei et al. [5] used is a single pulse-type stimulus.) The SR-like behavior can be seen clearly from Fig. 3(a), where the precision for three signals with different frequencies are shown for a large range of noise intensities. It is found that for each signal, there is an optimal noise intensity D_{opt} with which the maximal spike timing precision is obtained. The additional suitable noise increases the spiking probability and enhances the sensitive ability of the neuron to the stimulus. For a high noise level, the increasing stochastic nature of the noise dominates the firing dynamics of the neuron, which leads to the decrease of the spike timing precision. Clearly, the physical origin of such

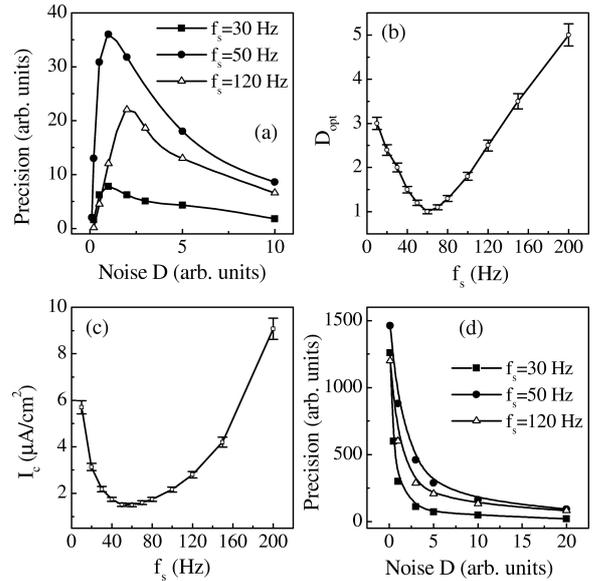


Fig. 3. (a) The spike timing precision versus different noise intensities D for three cases of deterministically subthreshold input signals with $I_1 = 1.0 \mu\text{A}/\text{cm}^2$ for $f_s = 30, 50$ and 120 Hz, respectively. (b) Optimal noise intensity D_{opt} versus signal frequency f_s for $I_1 = 1.0 \mu\text{A}/\text{cm}^2$. Error bars is added which calculated from 10 trials. (c) Critical signal amplitude I_c versus signal frequency f_s , error bars is added which calculated from 10 trials. (d) The spike timing precision versus different D for three cases of suprathreshold input signals $I_1 = 1.0 \mu\text{A}/\text{cm}^2$ for $f_s = 30, 50$ and 120 Hz, respectively.

a phenomenon is due to the mechanism of the SR [6]. The additional noise may result in the total effective input being suprathreshold which evokes the neurons to fire spikes locked timely to the maximum of the periodic signal. That is the firing of spikes associated with the noise. Fig. 3(b) summarizes the relation of frequency dependence of D_{opt} on f_s (for each signal frequency, the amplitude I_1 is fixed to $1 \mu\text{A}/\text{cm}^2$), which shows a nonmonotonous curve. It is worthy to note that the minimal value of D_{opt} is obtained for f_s near 50–60 Hz. This range is close to that of the intrinsic oscillation of the HH neuron. The nonmonotonous relation of D_{opt} on f_s is different from that of the bistable system [22], suggesting that the intrinsic oscillation may play an important role in affecting the dynamical behavior of SR.

In addition, when the amplitude I_1 of the periodic signal increases, we find that there exists a critical amplitude I_c for each signal frequency (see Fig. 3(c)),

above which the precision of the spike timing is monotonously degraded as the noise intensity D increases (see Fig. 3(d)), and the SR effect disappears. The critical amplitudes I_c obtaining for each signal frequency shows a nonmonotonous relation with f_s , and the minimal I_c is obtained for f_s near 50–60 Hz (see Fig. 3(c)). Noted that the value of I_c is almost equal to the critical value which divides the dynamics of noiseless HH neuron into nonfiring state and firing one [19]. Thus the signal with amplitude $I_1 > I_c$ can be viewed as superthreshold input. Two conclusions can be obtained: (1) For the noisy HH neuron with periodic forcing, there exists a critical I_c above which the SR effect disappears, and the added noise only increases the randomness of the firings of the neurons; (2) the critical amplitudes I_c for SR effect goes through a minimum as increasing the signal frequency f_s , which may be affected by the intrinsic oscillation of the HH neuron with natural frequency.

Therefore, the spike timing precision for the subthreshold periodic stimuli can be enhanced by suitable noise intensity via SR, whereas the precision for the suprathreshold periodic stimuli decreases monotonously as the noise intensity increases. The nonlinear resonance between the intrinsic oscillation of the neuron and the periodic signal produces the maximal response where only the small strength of the stimulus and the noise are needed.

More interestingly, the spike timing precisions of the array of neurons for signal with $f_s = 50$ Hz are always larger than those for signals with $f_s = 30$ and $f_s = 120$ Hz (see Figs. 3(a) and (c)). Fig. 4 summarizes this result (here all the signals are all subthreshold with $I_1 = 1$). It is found that at a low noise level the spike timing precisions for frequencies in the range of 30–100 Hz, especially around 50–60 Hz, have large values. This suggests that the signals with frequencies in such a range are encoded with high accuracy, indicating the existence of the frequency sensitivity. Such a frequency preference of 30–100 Hz with high spike timing precision may have important functional significance for the temporal encoding in brain. It may give a reason why many neural systems favor gamma rhythm (30–100 Hz) [23] both in higher brain functions and in lower level of information processing. From our previous work [19], we know that the nature frequency of the neuron reflected in the intrinsic oscillations is in the range of 40–70 Hz

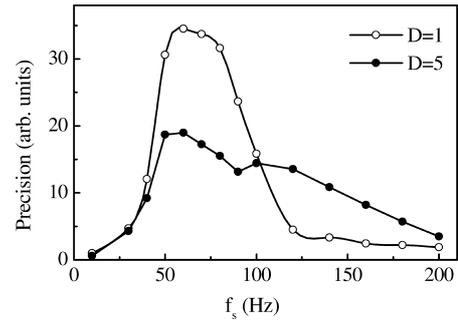


Fig. 4. The spike timing precision versus the signal frequencies f_s for a weak noise $D = 1$ and a large noise $D = 5$, respectively.

for different noise intensities. Physically, when the frequency of the input signal is close to the nature frequency of the HH oscillators, the resonance will occur. The maximum resonance arises by matching optimally the period of the input signal to that of the intrinsic oscillations of the neurons. Thus, due to resonance the neuron fires spikes with more strong coherence and more energy of the environment is transferred to the neuron, leading to a high precision of the spike timing near the maxima of the periodic signal. This is the physical reason why the frequency preference exists. Due to the existence of different types of rhythmic activities in the brain, the resonance and frequency preference may be the basic principles underlying the information processing and even in the realization of different behavioral and perceptual functions.

When the noise intensity increases to a large value, e.g., $D = 5$, the effect of stochastic nature of the noise on the responses of the neurons becomes large and even dominates the firing dynamics. Thus, the timing precisions for signals with frequencies in 30–100 Hz decays. However, there is still a frequency sensitive region. It is seen that the precisions for signals with high frequencies, i.e., $f_s > 100$ Hz, are larger than that for a small noise intensity $D = 1$. This is due to that the optimal noise intensity for signals with high frequencies is larger than that for signals with low frequencies (see Fig. 3(b)).

Furthermore, to quantify the synchronization of neuronal firings in the network, we introduce a coherence measure based on the normalized cross-correlations of pairs of neurons in the network [24]. The coherence between two neurons i and j is measured

by their cross-correlation of spike trains at zero time lag within a time bin of $\Delta t = \tau$. Suppose that a long time interval T is divided into many small bins with width τ and that two spike trains are given by $X(l) = 0$ or 1, $Y(l) = 0$ or 1, for $l = 1, 2, \dots, K$, with $T/K = \tau$. Thus, a coherence measure for a pair of neurons is defined as

$$k_{ij}(\tau) = \frac{\sum_{l=1}^K X(l)Y(l)}{\sqrt{\sum_{l=1}^K X(l) \sum_{l=1}^K Y(l)}}. \quad (8)$$

The population coherence measure $k(\tau)$ is defined by the average of $k_{ij}(\tau)$ over all pairs of neurons in the network. τ is taken as 1 ms in this Letter. We use this coherence measure to quantify the synchronization of the oscillations or coherent firings of the network.

We find that the population coherence of the firings for an intermediate noise intensity, e.g., $D = 1$, is larger than those for small (e.g., $D = 0.1$) and large noise intensity (e.g., $D = 10$) (see Figs. 2(b)–(d)). The measured coherence $k(\tau = 1)$ versus the noise intensity is shown in Fig. 5(a), which also displays a SR-like behavior, indicating that the coherence of the firings between the neurons is affected by the noise intensity. This coherence of the firings of the array maximized by a suitable noise is coincident with the enhancement of the spike timing precision.

Fig. 5(b) shows the coherence k of the array versus various frequencies f_s of the signals. As expected from the above findings, for a low noise level, i.e., $D = 1$, in the range of 30–100 Hz, the population coherence $k(\tau = 1)$ of the array has a large value, especially around 50–60 Hz, indicating the existence of frequency preference of the neural system in the encoding of the input signals. As discussed above, the enhancement of the population coherence results from the resonance between the intrinsic oscillation and the input signal. When the noise intensity increases, the coherence for the signal with frequency in 30–100 Hz decays. Finally, it is worthy to note that the frequency sensitive range found in the spike timing precision and population synchronization is similar to that found in signal detection and transduction [19]. This implies that the internal consistency of the enhancement of the abilities of the encoding, detection, transduction and synchronization of the network.

In conclusion, when a weak signal is input to such neural systems, the spike timing precision, and the re-

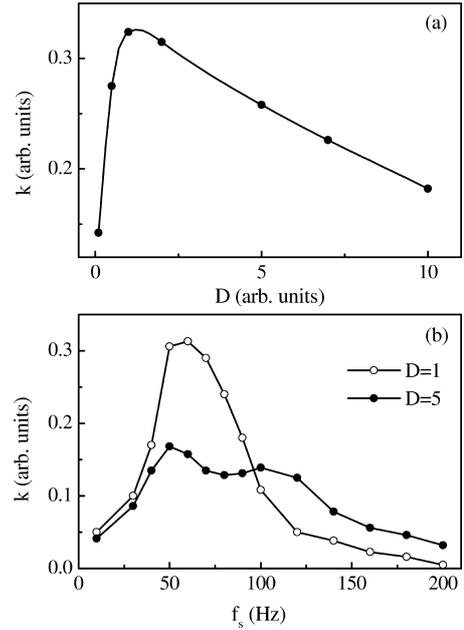


Fig. 5. (a) For a input signal ($f_s = 50$ Hz and $I_1 = 1.0 \mu\text{A}/\text{cm}^2$), the population coherence k versus different noise intensities D . (b) The population coherence k versus different signal frequencies f_s (all the signals have the same amplitude $I_1 = 1$) for $D = 1$ and $D = 5$, respectively.

sulted synchronization of the neurons can be maximized by the optimal noise intensity via SR. The dynamical features of SR shows a frequency dependence due to the effect of intrinsic oscillation. The optimal noise intensity D_{opt} and critical amplitude I_c for SR shows a global minimum locating at forcing frequency near 50–60 Hz. At the same time, resonance between the intrinsic oscillation and the signal enhances largely ability of encoding of the neuron to the signal, especially when the signal frequency is around that of the intrinsic oscillations. The population coherence measure of the network shows a significant increase when the frequency of signal in a frequency band centered around 50–60 Hz. Thus, the information processing can be carried out by the neurons with minimum expenditure of energy by the maximal resonance. Resonance improves the ability of neurons to respond selectively to inputs at preferred frequencies.

The dynamical features of a stochastic HH neuron with periodic forcing is similar to a periodically driven noisy underdamped bistable systems, as well studied recently by Alfonsi et al. [25], and cannot be simply

viewed as an overdamped motion of a point particle in a bistable potential [6] because of the existence of natural frequency characteristic. Due to the coexistence of multi-timescales controlled separately by intrinsic damped oscillation, noise-induced transition between wells, and the input periodic stimulus, the cooperation of these effects result in the maximal response of the system to signal as functions of the noise intensity and forcing frequency, respectively, leading to the coexistence of reported intrawell SR and interwell SR [25]. Noted that for an overdamped bistable system, there exists only interwell SR. That is, the optimal enhancement effect on the switching is obtained at a suitable noise level which produces a maximum cooperative between the noise-induced well-to-well transitions and the periodic signal.

The existence of the frequency sensitivity in the neural systems indicates that different inputs are able to be discriminated on the basis of their frequency content, and the synaptic oscillatory inputs near the resonant frequency produce the largest responses. Phenomenon of frequency preference has been actually observed in a number types of neurons such as various peripheral [26] and central neurons [7,8]. It was suggested that the intrinsic properties of such neurons may play important roles in determining the dynamics of coherent brain rhythmic activity and the realization of different behavioral and perceptual functions of the brain [3,10]. All these may give us an enlightenment why γ rhythms in various neural systems are popular in information processing and functional realization.

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