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Switching Role of Noise in the Aspect of Neuronal Reliability

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Abstract—Neuron in the cerebral cortex, which is said that a more higher-order function is governed, emits spikes very irregularly with low reliability. The question of why the brain works elaborately though such a seemingly probabilistic vague neurons has been studied for a long time. In this study, we study the effect of noise and oscillatory inputs from the aspect of neuronal reliability which is observed through Fano factor and investigate their roles in neural coding. We show that the noise switches its coding performance depending on the amplitude of oscillatory inputs.

1. Introduction

It is generally assumed that the information coding is done by the spike signal which is the neuronal responses. However, neuron in the cerebral cortex, which is said that a more higher-order function is governed, emits spikes very irregularly with low reproducibility[1]. On the other hand, neurons can fire with high temporal precision and reliability *in vitro*[2][3][4]. Information-theoretical analyses of the neuronal spike trains in several areas indicate that precise spike times contain more information about the stimulus than firing rate alone[5]. It is unknown how these precise spike times are used in the cerebral cortex[6][7][8]. Precisely timed reproducible spiking has been experimentally observed with a precision of milliseconds[9] which suggests the importance of precise spike timing in information processing.

Spike-time reliability is a measure for the reproducibility of individual spike times across trials[9]. Neurons produce a reliable sequence of spike times in response to some inputs and respond unreliably to others. In the *in vitro* slice, neurons fire reliably when injected with a random current containing high frequency components, but they fire unreliably when driven with a low pass or constant current[9][10]. Sinusoidally driven neurons show resonances in the reliability as a function of drive frequency [11].

Temporal spike coding schemes assume that neurons exchange information encoded by precisely timed spikes. Shadlen and Newsome showed that a short term firing rate can be reliably estimated by ensemble averaging of about hundred neurons (=population rate coding), without resorting to classical temporal averaging[1]. It is still controversial which coding scheme is used in the brain[12].

When we consider the coding scheme of seemingly probabilistic vague neurons, we can't help referring to the role of noise which plays an important role in neuronal coding. The improvement of signal transmission and detection through noise has been studied keenly over the past two decades under the paradigm of stochastic resonance[13]. Stochastic resonance is typically defined in terms of the signal-to-noise ratio in response to periodic stimulation. A long series of experiments has now firmly established that sensory neurons of various modalities benefit from ambient noise[14][15].

Periodic oscillatory rhythms, which emerge in the theory of stochastic resonance, also play important roles in neuronal coding. For example, theta phase precession has lead to the notion of phase coding that information is represented by the phase at which a cell fires. Indeed, it has been demonstrated that when estimating a rat's position from the firing of multiple place cells alone, the accuracy of estimation can be improved by taking the theta phase of firing into account[19]. Experimental data suggest that late firing in the theta cycle predicts upcoming positions on the rat's path whereas early firing in the cycle represents the rat's current position[20].

In this study, we speculate the correspondence between the effect of noise and rhythms from the aspect of neuronal reliability and investigate their roles in neural coding.

2. Fano factor and neuronal reliability

Fano factor is known as the ratio of the spike count variance to the spike count mean. Generally, Fano factor for a given counting window is useful for determining the irregularity of the point process. In order to use the Fano factor for quantifying the reliability of neurons, we set the size of the counting window small. In this case, a similar spike number per counting window makes the Fano factor small. For example, if the spike number is the same for all the trials, which means the perfectly reliable firing, Fano factor would be 0. In this way, high Fano factor indicates the low reliability of a neuron, and low Fano factor indicates the high reliability of a neuron.

In the concept of rate coding, the spike timings can be unreliable and inaccurate. On the other hand, in order to maintain the synchronicity for temporal coding, it is important that the neurons fire with high reliability and precision. Here, we can roughly define that high Fano factor corresponds to the rate coding, and low Fano factor corresponds to the temporal coding.

3. LIF with oscillatory and noisy inputs

The leaky integrate-and-fire model (LIF) neuron is likely the most widely studied of the abstract neuron models[1][16][21], especially in investigations of the neuronal code[16][17]. The main advantage of this model is its simplicity. We add the sinusoidal input for the common inputs to each trial, and the noise for the independent inputs to each trial. The model is depicted as

$$\dot{V}_i(t) = -V_i(t) + I_0 + A\sin(2\pi f t) + B\xi_i(t) + C\eta_i(t), \quad (1)$$

$$\text{if } V_i(t) = \theta, \text{ then } V_i(t+0) = V_0, \quad (2)$$

where $V_i(t)$, θ denote the membrane potential of ith trial and the threshold respectively. When the membrane potential $V_i(t)$ reaches the threshold θ, the neuron fires an action potential (a "spike") and instantly resets $V_i(t)$ to V_0. $\xi_i(t)$ is a Gaussian noise with ensemble-averaged quantities $\langle \xi_i(t) \rangle = 0$ and $\langle \xi_i(t)\xi_i(t') \rangle = \delta(t - t')$, and $\eta_i(t)$ is a colored noise which obeys Ornstein-Uhlenbeck process with ensemble-averaged quantities $\langle \eta_i(t) \rangle = 0$ and $\langle \eta_i(t)\eta_i(t') \rangle \propto \exp(-|t - t'|/s)$.

The parameter A, B, and C determine the amplitude of sinusoidal input, white noise, and colored noise respectively. We investigate how these parameters affect Fano factor in the next section.

4. Result

We first observe the case of the noisy state. The noisy state is realized when the oscillatory input term is weak and the noise term is strong. Figure 1 shows the Fano factor for a certain bin size Δ with 100 trials from equations (1) and (2).

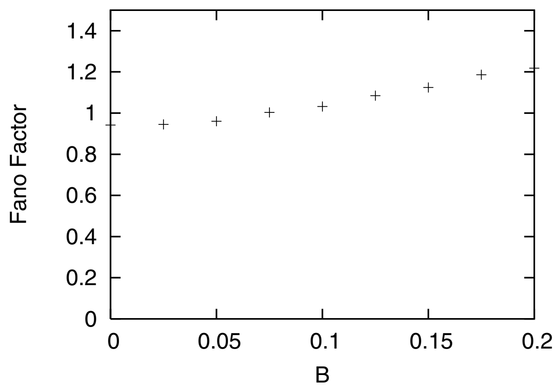

Figure 1: Fano factor in the noisy state obtained from equations (1) and (2). The parameters are set as $V_0 = 0, \theta = 1, I_0 = 0.9, A = 0.01, C = 0.1, f = 0.025, \Delta = 15$, respectively. Fano factor increases with increasing B.

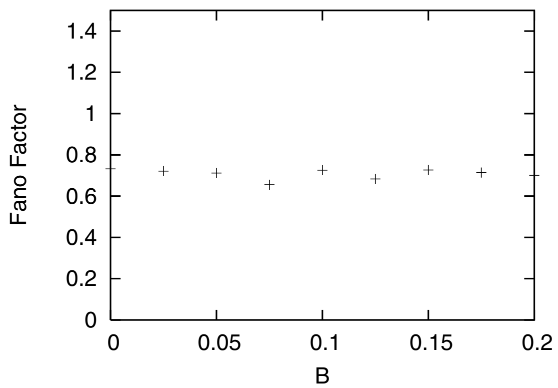

Figure 2: Fano factor in the quasi-noisy state obtained from equations (1) and (2). The parameters are set as $A = 0.03, C = 0.08$, respectively. Other parameters are set as the same as in the case of Figure 1. Fano factor is almost constant for increasing B.

Fano factor increases with increasing B when the oscillatory input is weak. When the oscillatory input is weak, spikes are generated by stochastic noise. Therefore, the rate of Fano factor is around unity, which means that it is almost random as a Poisson process and the reliability is low. Increasing the noise term B makes the firing more noisy, which makes the Fano factor increase. From the aspect of neural coding, the noise B plays a role for enhancing rate coding.

Next, we investigate the case of the quasi-noisy state. The quasi-noisy situation is realized when the oscillatory input term and the noise term is balanced. Figure 2 shows the Fano factor in the quasi-noisy state.

Fano factor is almost constant for increasing B in the quasi-noisy state. The rate of Fano factor is lower than that of the noisy state, since the ratio of the oscillatory inputs increased compared with the colored noise.

Figure 3 shows the Fano factor in the weak-noise state.

Fano factor shows a nonlinear correspondence with white noise. There is a local minimum in B = 0.075. When $B = 0$, the spike count for each trial is 0 or 1. When we increase B from $B = 0$ to $B = 0.075$, the spike count inside the bin for each trial is 1 for a great number of trials. This makes Fano factor decrease since the neuronal reliability increases. If we increase B further more from $B = 0.075$, 1 or 2 spikes in several trials are observed. When $B = 0.1375$, there is a small local minimum since the spike count is same number 2 for several trials. However, if we further increase B from $B = 0.1375$, Fano factor increases since the state of the neuron gradually shifts to the noisy state.

This nonlinear response is called stochastic resonance, typically defined in terms of the signal-to-noise ratio in response to periodic stimulation. When neurons are driven to fire at rates near frequency of the oscillation, they phase

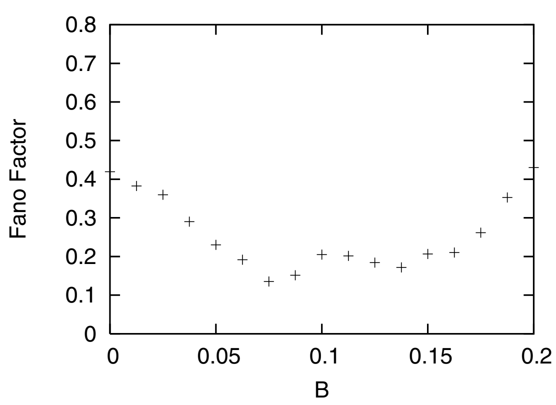

Figure 3: Fano factor in the weak-noise state obtained from equations (1) and (2). The parameters are set as $A = 0.1, C = 0.001$, respectively. Other parameters are set as the same as in the case of Figure 1 and 2. Fano factor shows a nonlinear correspondence with white noise, exhibiting stochastic resonance. There is a local minimum in B = 0.075.

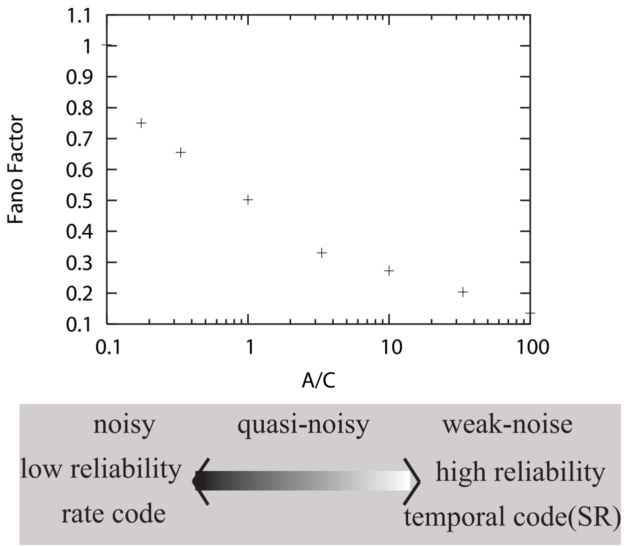

Figure 4: Fano factor for fixed noise strength B by modulating the ratio of the oscillatory input and the colored noise A/C in equations (1) and (2). The parameters are set as $B = 0.075$. The parameters A and C are both modulated at the same time from $A = 0.009$ to $A = 0.1$ and from $C = 0.09$ to $C = 0.001$ respectively, under the condition of preserving the average firing frequency at 25Hz. Other parameters are set as the same as in the case of Figure 1, 2, and 3. Fano factor monotonically decreases with increasing A/C.

lock with the periodic oscillation. This produces the reduction of spike-count variability and have been studied in several former studies of neuron models[22][23].

Figure 4 shows the Fano factor for fixed white noise strength B, and modulating the strength of periodicity A/C under the condition of preserving the average firing frequency.

Fano factor monotonically decreases with increasing A/C. When the parameter A/C is small, the neuron is in a noisy state and has low reliability so that it uses the concept of rate coding for information transfer. The white noise enhances the rate coding performance as we saw in Figure 1. As the parameter A/C increases, Fano factor decreases so that high reliability is realized by the weak-noise state neuron, and neurons use temporal coding. In this weak-noise state, neuron uses a stochastic resonance as we saw in Figure 3. The role of noise shifts its performance on both neuronal reliability and neural coding, depending on the strength of the oscillatory inputs A/C.

5. Discussion

We studied the effect of the noise and rhythms from the aspect of neuronal reliability. Neuronal reliability is defined by the rate of Fano factor with short time window. From the observation of Fano factor in several parameters changing input characteristics, we investigated the roles of the noise related to the performance of neural coding.

In a noisy state, asynchronous firing of cortical neurons induced by the white noise may play a positive role in the brain in a meaning different from stochastic resonance and coherence resonance. It plays a role for enhancing the ability of rate coding. This phenomenon has been studied by Masuda and Aihara in the concept of dual coding[12].

In a quasi-noisy state, the white noise had little effect on neuronal reliability. This state can be interpreted as the bifurcation point for a white noise in terms of its aspect of neural coding.

In a weak-noise state, neurons are driven to fire at rates near frequency of the oscillation, and they phase lock with the periodic oscillation and produces a saturation of the firing rate, reduction of spike-count variability. Neurons use the stochastic resonance for realizing high neuronal reliability. The white noise plays a key role for the stochastic resonance and the temporal coding in the brain. Its performance is completely different from that in a noisy state.

As in Figure 4, noise switches its coding performance depending on the amplitude of the oscillation. The amplitude of the oscillation is modulated by attention which raises the oscillatory activity in both spike trains and field potentials[18]. Three noise states in the previous section may correspond to the three level of attention. The noisy state corresponds to the low level of attention, and the weak-noise state corresponds to the high level of attention. According to our result, the white noise shifts its coding performance with respect to each attention level. For example, when the level of attention is high, neurons use the temporal coding scheme. Stochastic resonance may occur with a certain noise strength during the high level of attention.

It may be an important issue to investigate the correspondence between attention and coding performance.

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