Stimulus-Dependent Noise Facilitates Tracking Performances of Neuronal Networks

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Abstract. Understanding why neural systems can process information extremely fast is a fundamental question in theoretical neuroscience. The present study investigates the effect of noise on speeding up neural computation. We consider a computational task in which a neuronal network tracks a time-varying stimulus. Two network models with varying recurrent structures are explored, namely, neurons have weak sparse connections and have strong balanced interactions. It turns out that when the input noise is Poissonian, i.e., the noise strength is proportional to the mean of the input, the network have the best tracking performances. This is due to two good properties in the transient dynamics of the network associated with the Poissonian noise, which are: 1) the instant firing rate of the network is proportional to the mean of the external input when the network is at a stationary state; and 2) the stationary state of the network is insensitive to the stimulus change. These two properties enable the network to track the stimulus change rapidly. Simulation results confirm our theoretical analysis.

Keywords: Neural Computation, Stochastic Noise, Transient Dynamics, Tracking Speed, Balanced Network and Fokker-Planck equation.

1 Introduction

Neural systems can process information extremely fast. Taking the visual system of primates as an example, event-related potential study has revealed that human subjects are able to carry out some complex scenes analysis in less than 150 ms [1]. Neurophysiological recording showed that the latency of neural response can be as short as 40 ms in V1 [2], and $80 - 110$ ms in the temporal cortex [3]. Understanding why neural systems can perform computation in such a rapid speed is of critical importance in our understanding the computational mechanisms of brain functions.

Recent studies on the dynamics of neuronal populations have suggested that stochastic noise, which is observed ubiquitously in biological systems and is often thought to degrade information processing, may actually play a critical role in speeding up neural computation [4,5]. The idea is intuitively understandable. In

L. Zhang, J. Kwok, and B.-L. Lu (Eds.): ISNN 2010, Part I, LNCS 6063, pp. 1–8, 2010.

a noiseless environment, the speed of neural computation is limited by the membrane time constant of single neurons (in the order of $10 - 20$ ms). On the other hand, when inputs to a neural ensemble contain noises, noises can randomize the state of the network measured by the distribution of membrane potentials of all neurons. As a result, those neurons whose potentials are close to the threshold will fire rapidly after the onset of a stimulus, and conveys the stimulus information quickly to higher cortical areas. Although this computational picture has been widely recognized in the literature, there are some details concerning the performances of noises accelerating neural computation have not been well addressed, which particularly include: 1) the impact of noise structure, and 2) the impact of network topology, on the accelerating performance. The goal of this study is to investigate these two issues.

To demonstrate the computational speed of a network, we consider a tracking task in which the network tries to read-out a time-varying stimulus in time. We measure the discrepancy between the true stimulus values and the decoding results of the network. Two different noise forms, namely, the additive and the stimulus-dependent Gaussian white noises are compared.

2 The Models

The dynamics of a single neuron is modeled as an integrate-and-fire process, i.e.,

$$\tau \frac{dv_i}{dt} = -v_i + I_i(t), \tag{1}$$

where v_i represents the membrane potential of the ith neuron, τ the membrane time constant and $I_i(t)$ the synaptic current. A spike will be generated when the membrane potential of a neuron reaches a threshold θ, and immediately after firing, the membrane potential of the neuron is reset to be $v = 0$.

The synaptic current to a neuron is given by

$$I_i(t) = I_i^{rec}(t) + I_i^{ext}(t), \tag{2}$$

which consists of the recurrent input I_i^{rec} and the external input I_i^{ext}.

The recurrent input is given by

$$I_i^{rec}(t) = \sum_j w_{ij} \sum_m e^{-(t-t_j^m)/\tau_s}, \quad t_j^m \le t, \tag{3}$$

where w_{ij} is the connection weight from the jth neuron to the ith one, and τ_s the time constant of the synaptic current. t_j^m is the moment of the mth spike generated by the jth neuron. The form of w_{ij} is determined by the network topology.

The external input, which mimics the input current from other cortical or subcortical regions, is written as,

$$I_i^{ext}(t) = \mu + \sigma \xi_i(t), \tag{4}$$

where μ is the mean of the current and σ the noise strength. $\xi_i(t)$ is Gaussian white noise of zero mean and unit variance. The fluctuations of external inputs of different neurons are independent to each other, i.e., $<\xi_i(t_1)\xi_j(t_2)>=\delta_{ij}\delta(t_1-t_2)$, where the symbol $<\cdot>$ denotes averaging over many trials.

We are interested in two noise forms, namely, the additive and the stimulus-dependent noises. For the additive one, the noise strength σ^2 is a constant and independent of μ. For the stimulus-dependent one, $\sigma^2=\alpha\mu$. Note that when $\alpha=1$, the noise is Poisson. We call the general case of $\alpha\neq 1$ the Poissonian noise.

We consider two different network models.

Model 1: Weak sparse recurrent interaction. The network consists of only excitatory neurons. Denote N the number of neurons, $N\gg 1$. In order to keep neurons fire irregularly and at low firing rates (to be biologically plausible), neuronal connections need to be sparse and random. We choose two neurons have a probability p to be connected, and p is small, e.g., we may choose $p=0.1$, however, $Np\gg 1$ still holds. We set the weight $w_{ij}=1/(Np)$ if there is a connection between neuron i and j, and $w_{ij}=0$ otherwise. Thus, the total recurrent input to a neuron is in the order of one, and its fluctuations is in the order of $1/\sqrt{Np}$ and can be neglected.

Model 2: Strong balanced recurrent interaction. In a balanced network, neuronal connections are also sparse and random, however, the neuronal connection strength is much larger than that in Model 1. We set $w_{ij}\sim 1/\sqrt{NP}$. The total excitatory current to a neuron is then in the order of $\sqrt{NP}$, which needs to be balanced by inhibitory inputs, so that the overall recurrent input to a neuron is in the order of one. In the balanced network, the fluctuation of the overall recurrent input is in the order of one, which plays a critical role in driving the network dynamics.

3 Mean-Field Analysis

We apply mean-field approximation to analyze the population dynamics of two network models. For the convenience of analysis, we first consider there is no recurrent interaction between neurons and ignore the leakage term in the single neuron dynamics.

Denote $p(v,t)$ the distribution of membrane potentials of the neural ensemble. The Fokker-Planck equation for $p(v,t)$ is written as [6,7]

$$\tau\frac{\partial p(v,t)}{\partial t}=-\mu\frac{\partial p(v,t)}{\partial v}+\frac{\sigma^2}{2\tau}\frac{\partial^2 p(v,t)}{\partial t^2}. \tag{5}$$

The stationary distribution $p(v)$ of the network is calculated to be

$$p(v)=\begin{cases}\frac{1}{\theta}(1-e^{-2\tau\theta/\beta})e^{2\tau v/\beta} & v<0\\ \frac{1}{\theta}(1-e^{-2\tau(v-\theta)/\beta}) & 0\leq v\leq\theta\\ 0 & v>\theta\end{cases} \tag{6}$$

where

$$\beta = \sigma^2/\mu \tag{7}$$

is only the parameter determining the shape of $p(v)$.

The firing rate of the network is calculated to be

$$r = \frac{\sigma^2}{2\tau^2}\frac{\partial p(v)}{\partial v}|_\theta = \frac{\mu}{\theta\tau}. \tag{8}$$

From the above results, we observe two interesting properties: 1) the mean of the external input μ is linearly encoded by the firing rate r of the network in the stationary state. This property is independent of the noise structure. 2) When the noise is Poissonian, i.e., $\sigma^2 = \alpha\mu$, the parameter $\beta = \alpha$, is a constant and independent of the input strength μ. This is critical for fast computation. It implies that the stationary distribution of membrane potentials of the network is invariant with respect to the change of external inputs.

3.1 Population Dynamics of Model 1

Denote r the firing rate of each neuron. With the mean-field approximation, we calculate the mean and the variance of recurrent input to a neuron, which are

$$\begin{aligned} < \sum_j w_{ij} \sum_m e^{-(t-t_j^m)/\tau_s} > &\approx Np\frac{1}{Np} < \int_{-\infty}^t e^{-(t-t')/\tau_s} dW > \\ &= r\tau_s, \qquad (9) \\ D(\sum_j w_{ij} \sum_m e^{-(t-t_j^m/\tau_s)}) &= \frac{Np}{(Np)^2} D(\int_{-\infty}^t e^{-(t-t')/\tau_s} dW) \\ &\approx 0, \qquad (10) \end{aligned}$$

where dW denotes a diffusion approximation of the Poisson process and the symbol $D(x)$ the variance of x.

Combining with the external input, the dynamics of a single neuron is written as,

$$\tau\frac{dv_i}{dt} = -v_i + (\mu + r\tau_s) + \sigma\xi_i. \tag{11}$$

Thus, under the mean-field approximation, the effect of the recurrent interaction is equivalent to changing the mean of the synaptic input to a neuron from μ to $\mu + r\tau_s$. Based on the above calculation, the stationary distribution of membrane potentials of the network is given by Eq.(6), and the corresponding shape parameter β and the network firing rate r_n are calculated to be

$$\beta = \frac{\sigma^2}{\mu + r\tau_s}, \tag{12}$$

$$r_n = \frac{\sigma^2}{2\tau^2}\frac{\partial p(v)}{\partial v}|_\theta = \frac{\mu + r\tau_s}{\theta\tau}. \tag{13}$$

In the stationary state, the network firing rate r_n (averaged over the neural population) equals to the firing rate r of individual neurons (averaged over time). From Eq.(13), it gives

$$r = \frac{\mu}{\theta\tau - \tau_s}, \tag{14}$$

and hence

$$\beta = \frac{(\theta\tau - \tau_s)\sigma^2}{\theta\tau\mu}. \tag{15}$$

Again, we observe two good properties: 1) the mean of the externa input is linearly encoded by the firing rate of the network in the stationary state; and 2) when the noise is Poissonian, $\beta = \alpha(\theta\tau - \tau_s)/(\theta\tau)$, the distribution of membrane potentials of the network is independent of the input strength μ.

3.2 Population Dynamics of Model 2

Denote N_E and N_I the numbers of excitatory and inhibitory neurons in the network, respectively, and $K_E = pN_E$ and $K_I = pN_I$ the average numbers of excitatory and inhibitory connections a neuron may receive. We set $w_{ij}^{EE} = J_E/\sqrt{K_E}$, and $w_{kl}^{IE} = J_E/\sqrt{K_E}$, with a probability p and zero otherwise, and set $w_{ij}^{II} = -J_I/\sqrt{K_I}$, and $w_{kl}^{EI} = -J_I/\sqrt{K_I}$ if two neurons have a connection (with a probability p) and zero otherwise. r_E and r_I represent the firing rates of excitatory and inhibitory neurons.

With the mean-field approximation, the mean and the variance of a neuron's recurrent inputs are calculated to be,

$$< \sum_j w_{ij}^{ab} \sum_m e^{-(t-t_{j,b}^m)/\tau_{b,s}} > = \sqrt{K_b} J_b r_b \tau_{b,s}, \tag{16}$$

$$D(\sum_j w_{ij}^{ab} \sum_m e^{-(t-t_{j,b}^m)/\tau_{b,s}}) = \frac{(J_b)^2 r_b \tau_{b,s}}{2}, \tag{17}$$

where the variables a and b represent E or I.

Combining with the external inputs, we have

$$\begin{aligned} \tau_E \frac{dv_{i,E}}{dt} &= -v_i + (\mu + \sqrt{K_E} J_E r_E \tau_{E,s} + \sqrt{K_I} J_I r_I \tau_{I,s}) \\ &+ \sqrt{\sigma^2 + \frac{(J_E)^2 r_E \tau_{E,s}}{2} + \frac{(J_I)^2 r_I \tau_{I,s}}{2}} \xi_i, \end{aligned} \tag{18}$$

$$\begin{aligned} \tau_I \frac{dv_{i,I}}{dt} &= -v_i + (\sqrt{K_E} J_E r_E \tau_{E,s} + \sqrt{K_I} J_I r_I \tau_{I,s}) \\ &+ \sqrt{\frac{(J_E)^2 r_E \tau_{E,s}}{2} + \frac{(J_I)^2 r_I \tau_{I,s}}{2}} \xi_i. \end{aligned} \tag{19}$$

Thus, under the mean-field approximation, the effect of recurrent interactions in the balanced network is equivalent to changing the mean and the variance of the synaptic input properly. Following the same calculations as in Model 1, the stationary distributions of membrane potentials of the excitatory and inhibitory neuron pools satisfy the same distribution as in Eq.(6), except that the shape parameters β_E and β_I are changed accordingly, which are,

$$\beta_E = \frac{\sigma^2 + 0.5(J_E)^2 r_E \tau_{E,s} + 0.5(J_I)^2 r_I \tau_{I,s}}{\mu + \sqrt{K_E} J_E r_E \tau_{E,s} + \sqrt{K_I} J_I r_I \tau_{I,s}}, \tag{20}$$

$$\beta_I = \frac{(J_E)^2 r_E \tau_{E,s} + (J_I)^2 r_I \tau_{I,s}}{2\sqrt{K_E} J_E r_E \tau_{E,s} + 2\sqrt{K_I} J_I r_I \tau_{I,s}}. \tag{21}$$

The firing rate of each neuron pool, which equals to the firing rate of individual neurons in the stationary state, is calculated to be:

$$r_E = \frac{\mu + \sqrt{K_E} J_E r_E \tau_{E,s} + \sqrt{K_I} J_I r_I \tau_{I,s}}{\theta \tau_E}, \tag{22}$$

$$r_I = \frac{\sqrt{K_E} J_E r_E \tau_{E,s} + \sqrt{K_I} J_I r_I \tau_{I,s}}{\theta \tau_I} \tag{23}$$

By the self-consistent condition, we have

$$r_E = \frac{\theta \tau_I - J_I \sqrt{K_I} \tau_{I,s}}{\theta^2 \tau_E \tau_I - \theta \tau_E J_I \sqrt{K_I} \tau_{I,s} - \theta \tau_I J_E \sqrt{K_E} \tau_{E,s}} \mu \tag{24}$$

$$r_I = \frac{J_E \sqrt{K_E} \tau_{E,s}}{\theta^2 \tau_E \tau_I - \theta \tau_E J_I \sqrt{K_I} \tau_{I,s} - \theta \tau_I J_E \sqrt{K_E} \tau_{E,s}} \mu \tag{25}$$

Thus, in the balanced network, the mean of the external input is linearly encoded by the firing rate of the network.

When the noise is Poissonian, we get

$$\begin{aligned} \beta_E = & \frac{(J_E)^2 \theta \tau_{E,s} \tau_I - (J_E)^2 J_I \tau_{E,s} \tau_{I,s} \sqrt{K_I} + (J_I)^2 J_E \tau_{E,s} \tau_{I,s} \sqrt{K_E}}{2\theta^2 \tau_E \tau_I - 2\theta J_I \sqrt{K_I} \tau_{I,s} \tau_E} \\ & + \frac{\alpha(\theta \tau_E \tau_I - J_E \sqrt{K_E} \tau_{E,s} \tau_I - J_I \sqrt{K_I} \tau_{I,s} \tau_E)}{\theta \tau_E \tau_I - J_I \sqrt{K_I} \tau_{I,s} \tau_E}, \end{aligned} \tag{26}$$

$$\beta_I = \frac{J_E \theta \tau_{E,s} \tau_I - J_E J_I \tau_{E,s} \tau_{I,s} \sqrt{K_I} + (J_I)^2 \tau_{E,s} \tau_{I,s} \sqrt{K_E}}{2\sqrt{K_E} \tau_I \tau_{E,s} \theta}. \tag{27}$$

Both β_E and β_I are independent of the mean of the external input.

4 Tracking a Time-Varying Stimulus

In a noise environment, since individual neurons fire irregularly, it is the statistical properties of network response that encodes external stimuli. Furthermore, for fast computation, it is the transient dynamics of the network that conveys the stimulus information. The transient dynamics of a network is affected by the noise form and the initial state of the network. In order to achieve fast and

Table 1. The fitted parameters

	Model 1	Model 2
Poissonian Noise	$a = 0.83, \phi = -0.04$	$a = 0.94, \phi = -0.09$
Additive Noise	$a = 0.67, \phi = -0.42$	$a = 0.90, \phi = -0.20$

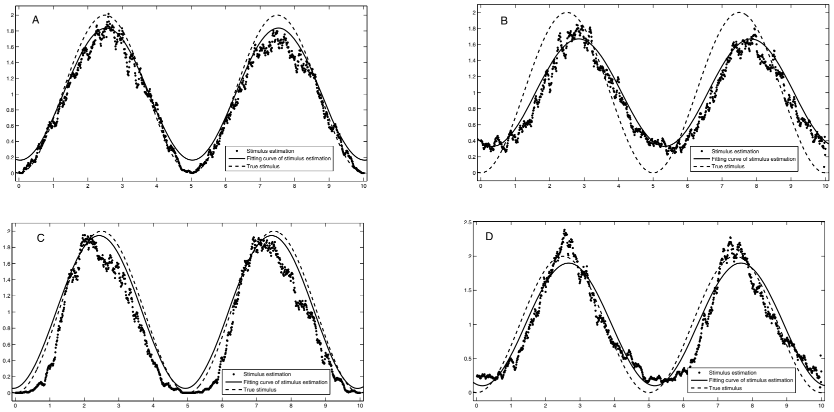

Fig. 1. Tracking performances of two network models. $T = 5\tau$.(A) Model 1 with the Poissonian noise; (B) Model 1 with the additive noise; (C) Model 2 with the Poissonian noise; and (D) Model 2 with the additive noise.

reliable computation, it is important that the statistical properties of the transient dynamics of a network is insensitive to input changes. So, what kind of noise structure is most suitable for fast neural computation, in particular, for the tracking task we consider?

In the above analysis, for two network models, we have found that when the input noise is Poissonian, the network transient dynamics has two important properties, which are: 1) the mean of external input is linearly encoded by the instant firing rate of the network when the network is at a stationary state; and 2) the stationary state of the network is insensitive to the change of the stimulus value (the mean of external input). These two good properties ensure that the Poissonian noise is ideal for fast tracking. In the fast tracking process, the stimulus value changes rapidly. The fact that the stationary state of the network is insensitive to the stimulus value implies that the network is always in a good state to catch up with the change; otherwise, the network has to evolve its state to a stationary one which is time-consuming.

We carry out simulation to confirm our theoretical analysis. We consider the mean of the external input changes with time, i.e, $\mu = 1 - cos(2\pi t/T)$. The parameter T controls the change speed of the stimulus. We measure firing rates of the network at different time, and fit them with a function $r = 1 - acos(2\pi t/T + \phi)$. The phase ϕ, which typically has a negative value, reflects the amount of delay in tracking. The deviation of a from the value one reflects the discrepancy between the network decoding and the true stimulus. Apparently, the closer the value of ϕ to zero and the value of a to one, the better the tracking performance is.

Fig. 1 illustrates the tracking performances of two network models with $T = 5\tau$ and varied noise forms. The additive noise strength is set to be $\sigma^2 = 1$. The fitted parameters are summarized in Table 1. We see that for two network models, the tracking performances in the case of the Poissonian noise are better than that in the case of the additive noise.

5 Conclusions

The present study investigates the ideal noisy environment for fast neural computation. We observe that the stimulus-dependent Poissonian noise, rather than stimulus-independent ones, has the best effect of accelerating neural information processing. This property is also intuitively understandable. For the strong diffusive noise, in a short time-window, it is fluctuations, rather than the mean drift, that dominates the value of external inputs (that is, $W(t) \approx \mu t + \sigma\eta\sqrt{t} \approx \sigma\eta\sqrt{t}$, for $t \ll 1$, where η is a Gaussian random number of zero mean and unit variance). The signal-noise correlation is the key that enables the stimulus information to be adequately propagated to the neural system quickly.

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