Impact of noise structure and network topology on tracking speed of neural networks

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\textbf{A B S T R A C T}

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 accelerating neural computation. To evaluate the speed of network response, we consider a computational task in which the network tracks time-varying stimuli. Two noise structures are compared, namely, the stimulus-dependent and stimulus-independent noises. Based on a simple linear integrate-and-fire model, we theoretically analyze the network dynamics, and find that the stimulus-dependent noise, whose variance is proportional to the mean of external inputs, has better effect on speeding up network computation. This is due to two good properties in the transient network dynamics: (1) the instant firing rate of the network is proportional to the mean of external inputs, and (2) the stationary state of the network is robust to stimulus changes. We investigate two network models with varying recurrent interactions, and find that recurrent interactions tend to slow down the tracking speed of the network. When the biologically plausible Hodgkin–Huxley model is considered, we also observe that the stimulus-dependent noise accelerates neural computation, although the improvement is smaller than that in the case of linear integrate-and-fire model.

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1. Introduction

Neural systems can process information extremely fast. Given the visual system of primates as an example, event-related potential study has revealed that human subjects are able to carry out some complex scene analysis in less than 150 ms (Thorpe, Fize, & Marlot, 1996). Single unit recording showed that the latency of neural response in V1 can be as short as 40 ms (Celebrini, Thorpe, Trotter, & Imbert, 1993; Raiguel, Xiao, Marcar, & Orban, 1999; Schmolesky et al., 1998) and in the temporal cortex 80–110 ms (Sugase, Yamane, Ueno, & Kawano, 1999). Understanding why neural systems can perform computation in such a rapid speed is of critical importance in our understanding of the computational mechanisms of brain functions.

A big obstacle to fast neural computation comes from the slow dynamics in single neurons, which is typically in the order of 10–20 ms. Taking into account that neural signals are propagated through more than ten layers from retina to V1 (Kandel, Schwartz, Jessell, Mack, & Dodd, 1991), it is hard to explain the short latency observed in V1. Recent studies 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 (Amit & Brunel, 1997; Destexhe, Rudolph, & Pare, 2003; Gerstner, 2000; Knight, 1972; Van Rossum, Turrigiano, & Nelson, 2002; Vreeswijk & Sompolinsky, 1996). The idea is intuitively understandable. Consider a neural population encodes the stimulus information. Noises randomize the state of the neural ensemble, i.e., the distribution of neuronal membrane potentials. Consequently, those neurons whose potentials are close to the threshold will fire rapidly after the onset of a stimulus, conveying the stimulus information quickly to higher cortical areas.

Although the above picture concerning the role of noise in accelerating neural computation has been widely recognized in the literature, there are some details about the implementation of this strategy in practice need to be carefully clarified. In a fast computation paradigm, it is transient response of a network that encodes the stimulus information. The transient dynamics of a network is sensitive to its initial state, the noise structure and the network topology. For the same input, the network response...
can be significantly different when its initial state varies. Thus, to really achieve fast computation based on noise, it is crucial that the transient response of a network exhibits statistical features which are repeatable and robust with respect to input fluctuations. This requirement sets conditions on the structure of noise and network topology suitable for fast computation. The goal of this work is to investigate these issues.

To evaluate the speed of neural computation, we consider a computational task in which a network tracks time-varying stimuli. We measure the reaction time and the delay in tracking to quantify the response speed of the network. For the noise resource, we consider it is from external inputs. In reality, spontaneous synaptic activity can also induce noise and contribute to speed up neural response (Destexhe et al., 2003), but this is not in the scope of the present study. Two noise forms are compared, namely, the stimulus-dependent and stimulus-independent Gaussian white noises. For the stimulus-dependent noise, the variance of noise is proportional to the mean of external inputs. We find that in the presence of stimulus-dependent noise, the network activity exhibits two computationally desirable properties, which are: (1) the firing rate of the network at stationary states linearly encodes the mean of external inputs, and (2) the stationary states of the network are rather insensitive to the change of input. These two properties enable the network to track time-varying stimuli much quicker than that with the stimulus-independent noise. We investigate two network models with varying topologies, namely, neurons having sparse-weak and balanced-strong recurrent interactions. We find that the tracking performance of the network, measured by the tracking speed of the network to time-varying stimuli, is degraded with the strength of recurrent interactions. Part of the results in this work will appear in Huang and Wu (2010).

The organization of the paper is as follows. In Section 2, we first introduce the network models used in this study. In Section 3, we apply the mean-field approximation to analyze the statistical properties of network responses. In Section 4, general conditions for fast computation are discussed. In Section 5, numerical simulations are carried out to validate our theoretical analysis. In Section 6, overall discussions and conclusions about this work are given.

2. Methods

2.1. Dynamics of single neurons

Two different neuron models have been used in the present study, one is the linear integrate-and-fire (IF) model and the other Hodgkin–Huxley (HH) model. By using the simple linear IF neuron, we solve the network dynamics analytically, which gives us insight into the mechanism underlying fast neural computation. We carry out simulation with the biologically plausible HH model to further confirm our theoretical analysis.

2.1.1. Linear integrate-and-fire neuron

For the linear IF model, the dynamics of a single neuron is written as Fusi and Mattia (1999)

\[
\tau \frac{dv}{dt} = I(t).
\]

A spike will be generated when the membrane potential of a neuron reaches a threshold \(v_{th}\), after that the membrane potential of the neuron is reset to be \(v = v_{reset}\). Without loss of generality, we choose \(v_{th} = 1\) and \(v_{reset} = 0\). Note that the linear IF model does not contain a leakage term.

The total synaptic current to a neuron is given by

\[
I(t) = I^{rec}(t) + I^{ext}(t),
\]

which consists of the recurrent input \(I^{rec}\) and the external one \(I^{ext}\).

The recurrent input represents the synaptic currents from other neurons in the network, which is given by

\[
I^{rec}(t) = \sum_{j} w_{ij} \sum_{m} e^{-\left(\frac{t-t_{m}^j}{\tau}\right)} , \quad t_{m}^j \leq t, (3)
\]

where \(w_{ij}\) is the connection weight from the jth neuron to the ith one, \(\tau_j\) the time constant of the synaptic current, and \(t_{m}^j\) the moment of the mth spike generated by the jth neuron. The connection weight \(w_{ij}\) is determined by the network topology.

2.1.2. Hodgkin–Huxley neuron

For the HH model, the dynamics of a single neuron is written as

\[
C_n \frac{dv}{dt} = -I_n + I^{rec} + I^{ext},
\]

(4)

where \(C_n = 1 \mu F/cm^2\) is the membrane capacitance and \(I^{ext}\) is the external input. The membrane current \(I_n\) is composed of a leakage term, a delayed rectified \(K^+\) current and a transient \(Na^+\) current, that is,

\[
I_n^L = g_{L}(v - E_{L}) + g_{Na} m^{3} h(v - E_{Na}),
\]

(5)

The maximal conductances and reversal potentials used in the model are \(g_{L} = 0.1 \text{ mS/cm}^2, g_{K} = 9 \text{ mS/cm}^2, g_{Na} = 35 \text{ mS/cm}^2, E_{L} = -65 \text{ mV}, E_{K} = -90 \text{ mV}\) and \(E_{Na} = 55 \text{ mV}\).

The gating variables, \(m, n, h\), obey a first-order kinetics of the following form (take the activation variable \(n\) for example),

\[
\frac{dn}{dt} = A(e_{n}(v)(1 - n) - \beta_{n}(V)n),
\]

(6)

where \(e_{n}(V) = 0.01(V + 34)/(1 - \exp(-0.1(V + 34))), \beta_{n}(V) = 0.125 \exp(-(V + 44)/80)\). For the activation variable \(m, e_{m}(V) = -0.1(V + 35)/(\exp(-0.1(V + 35)) - 1), \beta_{m}(V) = 4\exp(V + 60)/18\); and for the inactivation variable \(h, e_{h}(V) = 0.07 \exp((V + 58)/20), \beta_{h}(V) = 1/(\exp(-0.1(V + 28) + 1))\). \(A\) is a constant, which is chosen to be 5.

We adopt the kinetic parameters and maximal conductances according to Wang and Buzsaki (1996), which are modified from Hodgkin and Huxley (1952). The recurrent synaptic current is given by

\[
I^{rec}(t) = \sum_{j=1}^{N} g_{syn}(v_i(t) - E_{syn}) s_j(t),
\]

(7)

where \(E_{syn}\) is the reversal potential and \(g_{syn}\) the maximal synaptic conductance. Typically, these two parameters are set as \(E_{syn} = 0 \text{ mV}\) and \(g_{syn} = 0.01 \text{ mS/cm}^2\), which indicates that the connections are excitatory but weak. The maximal synaptic conductance is divided by average number of synaptic inputs per neuron, so that when the number of synapses is varied, the total synaptic drive per cell in average remains the same. The variable \(s_j\) represents the fraction of open synaptic ion channels on the synapse from the jth neuron to the ith one.

The dynamics of \(s_j\) obeys a first-order kinetic (Perkel, Mulloney, & Budelli, 1981; Wang & Rinzel, 1993)

\[
\frac{ds_j}{dt} = \alpha F(v_{pre}^{j})(1 - s_j) - \beta s_j,
\]

(8)

where \(F(v_{pre}^{j}) = 1/(1 + \exp(-v_{pre}^{j} - \theta_{syn}/2))\) is an instantaneous and sigmoidal function of the presynaptic membrane potential which represents the normalized concentration of the postsynaptic transmitter–receptor complex. \(\theta_{syn}\) is set to 0 mV. The channel opening rate \(\alpha = 12 \text{ ms}^{-1}\) and the channel closing rate \(\beta = 0.1 \text{ ms}^{-1}\). The picture for the synapse model is quite straightforward, transmitter release occurs only when the presynaptic neuron emits a spike (guaranteed by a high enough \(\theta_{syn}\)), then there will be a fast rise of \(g_{syn}\); at other time, \(s_j\) will decay to zero in synaptic time constant \(\tau_{syn} = 1/\beta = 10 \text{ ms}\).
2.2. Structures of input noises

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

\[ I_{i}^{\text{ext}}(t) = \mu(t) + \sigma(t) \xi_i(t), \]  

where \( \mu(t) \) is the mean of the current, and \( \xi_i(t) \) is the Gaussian white noise of zero mean and unit variance. \( \sigma(t) \) is a scaling factor, which represents the noise strength. The fluctuations of external inputs are independent to each other, i.e., \( \langle \xi_i(t) \rangle = 0 \) and \( \langle \xi_i(t_1) \xi_j(t_2) \rangle = \delta_{ij}(t_1 - t_2) \), where the symbol \( \langle \cdot \rangle \) denotes averaging over many trials.

We are interested in two noise forms, namely, the stimulus-independent and stimulus-dependent Gaussian white noises. For the former, the noise strength \( \sigma(t)^2 = \sigma^2 \) is a constant and independent of \( \mu(t) \). For the latter, the noise strength is proportional to the mean of external inputs, i.e., \( \sigma(t)^2 = \alpha \mu(t) \). When \( \alpha = 1 \), the noise can be regarded as a diffusion approximation of the Poisson point process.

2.3. Network structures

Two kinds of network models are considered in the following study. They have different neuronal recurrent structures, namely, sparse-weak and balanced-strong interactions.

Network 1: Sparse-weak recurrent interactions.

This network consists of only excitatory neurons. Denote \( N \) the number of neurons in the network, \( N \gg 1 \). In order to keep neurons fire irregularly and at low firing rates (being biologically plausible), neuronal connections are sparse and random. The probability that a pair of neurons are connected in either direction is denoted as \( p \). The value of \( p \) is small, implying that neuronal connections are sparse, e.g., \( p = 0.1 \), however, \( Np \gg 1 \) still holds. We set the weight \( w_{ij} = 1/(Np) \) if there is a connection from neuron \( j \) to \( i \), and otherwise \( w_{ij} = 0 \). The total recurrent input to neuron \( i \) is then in the order of unit, and its fluctuation can be neglected (which is in the order of \( 1/N \)). The dynamics of a neuron in this network could be described as

\[ \tau_E \frac{d v_i}{dt} = \sum_j w_{ij} \sum_m e^{-\frac{(t-t_{ij})}{\tau_E}} + I_{i}^{\text{ext}}, \quad t_{ij}^m \leq t. \]  

Network 2: Balanced-strong recurrent interactions.

In this network, neuronal connections are also sparse and random, however, the connection strength is strong. We set \( w_{ij} \sim 1/\sqrt{NP} \). Thus the excitatory current to a neuron is in the order of \( \sqrt{NP} \), which needs to be balanced by inhibitory inputs, so that the overall recurrent current to a neuron is still in the order of unit. In a balanced network, the fluctuation of the total recurrent current is in the order of unit, which plays a critical role in driving the network dynamics (Shadlen & Newsome, 1995; Vreeswijk & Sompolinsky, 1996).

Hereafter, we use either sub- or super-scripts \( E \) and \( I \) to differentiate variables and parameters associated with excitatory and inhibitory neurons. For instance, we use \( \tau_E \) to denote the membrane potential time constant for an excitatory neuron, and \( \tau_I \) for an inhibitory one. We use \( w_{ij}^{E} \) to represent the recurrent interaction from an inhibitory neuron to an excitatory one. The meanings of \( w_{ij}^{E} \), \( w_{ij}^{I} \), \( w_{ij}^{E,E} \), \( w_{ij}^{E,I} \), \( \tau_E \), and \( \tau_I \) are similarly defined. For the linear IF model, the dynamics of an excitatory and an inhibitory neurons are written as

\[ \tau_E \frac{d v_i}{dt} = \sum_j w_{ij}^{E} \sum_m e^{-\frac{(t-t_{ij}^m)}{\tau_E}}, \quad \tau_I \frac{d v_i}{dt} = \sum_j w_{ij}^{I} \sum_m e^{-\frac{(t-t_{ij}^m)}{\tau_I}} + I_{i}^{\text{ext}}, \quad t_{ij}^m \leq t, \]  

\[ \tau_E \frac{d v_i}{dt} = \sum_j w_{ij}^{E} \sum_m e^{-\frac{(t-t_{ij}^m)}{\tau_E}} + I_{i}^{\text{ext}}, \quad t_{ij}^m \leq t. \]  

Here, only excitatory neurons receive external inputs.

3. Theoretical analysis

In this section, we analyze the dynamics of networks with linear IF neurons.

3.1. Distribution of neuronal membrane potentials

To start, we consider there is no recurrent interaction between neurons. Denote \( p(v, t) \) the distribution of neuronal membrane potentials, i.e., \( p(v, t)dv \) is the fraction of neurons with potentials in the range of \([v, v + dv]\) at time \( t \). The time evolution of \( p(v, t) \) is governed by both the mean and fluctuation of external inputs according to the Fokker–Planck equation (Risken, 1996; Tuckwell, 1988).

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

At a stationary state, \( p(v, t) \) satisfies a set of boundary conditions (Brunel & Hakim, 1999), which are

\[ p(\theta, t) = 0, \]  

\[ \frac{\partial p(\theta, t)}{\partial v} = -2\tau r(t), \]  

\[ \frac{\partial p(v_{\text{reset}}^+)}{\partial v} - \frac{\partial p(v_{\text{reset}}^-)}{\partial v} = -2\tau r(t), \]  

where \( \partial p(v_{\text{reset}}^+)/\partial v \) and \( \partial p(v_{\text{reset}}^-)/\partial v \) denote the left and the right derivative of \( p(v) \) at \( v_{\text{reset}} \), respectively. For more details about the setting of these boundary conditions, please refer to Brunel and Hakim (1999).

Combining with the normalization condition, i.e., \( \int_{-\infty}^{\infty} p(v)dv = 1 \), the stationary distribution of the network can be exactly solved, which is

\[ p(v) = \begin{cases} \frac{1}{\theta} (1 - e^{-\frac{v}{\beta}/\theta}) e^{\frac{v}{\beta}} & v < 0 \\ \frac{1}{\theta} (1 - e^{-\frac{v-\theta}{\beta}}) & 0 \leq v \leq \theta \\ 0 & v > \theta, \end{cases} \]  

where

\[ \beta = \frac{\sigma^2}{\mu}. \]  

In this study, we consider the parameters \( \tau \) and \( \theta \) are fixed, hence the shape of \( p(v) \) is determined by the parameter \( \beta \). The profile of \( p(v) \) is shown in Fig. 1. We may note that if spontaneous synaptic activity in a single neuron is included, \( \tau \) and \( \theta \) may change with neuronal states (Destexhe et al., 2003).

The firing rate of the network is calculated to be

\[ r = \frac{1}{2\pi^2} \frac{\partial^2 p(v)}{\partial v^2} \bigg|_{\theta}, \]  

\[ = \frac{\sigma^2}{\theta r^2 \beta}, \]  

\[ = \frac{\mu}{\theta}. \]
Thus, under the mean-field approximation, the effect of recurrent interactions is equivalent to changing the mean of synaptic input from $\mu$ to $\mu + r\tau_s$.

Based on the calculation in Section 3.1, the stationary state of the network is given by Eq. (17), and the corresponding shape parameter $\beta$ and the population firing rate $r_n$ are calculated to be

$$\beta = \frac{\alpha^2}{\mu + r\tau_s},$$

$$r_n = \left. \frac{1}{\theta} \frac{\sigma^2}{2\sqrt{\pi}} \frac{\partial p(v)}{\partial v} \right|_{v=0},$$

$$= \frac{\mu + r\tau_s}{\theta\tau_s}.$$  

In the stationary state, the population firing rate $r_n$ (averaged over the neural ensemble) equals the instantaneous firing rate $r$ of individual neurons (averaged over time). From Eq. (24), we get

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

and hence

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

Again, we observe two desirable properties: (1) the mean of the external input is linearly encoded by the firing rate of the network in a stationary state, and (2) when the noise is stimulus-dependent, $\beta = \alpha(\theta\tau - \tau_s)/(\theta\tau)$, that is, the distribution of membrane potentials of the network is independent of $\mu$.

### 3.2.2. Population dynamics of Network 2

Denote $N_E$ and $N_I$ the numbers of excitatory and inhibitory neurons in the network, and $K_E = pN_E$ and $K_I = pN_I$ the average numbers of excitatory and inhibitory connections of a neuron receives, respectively. We set $w_{ij}^{EE} = j_z / \sqrt{K_E}$, and $w_{ij}^{EI} = j_z / \sqrt{K_E}$, with a probability $p$ and zero otherwise, and set $w_{ij}^{II} = -j_z / \sqrt{K_I}$ and $w_{ij}^{IE} = -j_z / \sqrt{K_I}$, with a probability $p$ and zero otherwise. $r_E$ and $r_I$ represent the firing rates of excitatory and inhibitory neurons, respectively.

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

$$\left\langle \sum_j w_{ij}^{\alpha \beta} \sum_m e^{-(t-t_j)m/\tau_\alpha} \right\rangle \approx \frac{Np}{2Np} \left\langle \int_{-\infty}^{\tau_E} e^{-(t-t')/\tau_\alpha} r dt' \right\rangle = r_\tau,$$

$$D\left\langle \sum_j w_{ij}^{\alpha \beta} \sum_m e^{-(t-t_j)m/\tau_\beta} \right\rangle \approx \frac{Np}{\sqrt{2Np}} D\left\langle \int_{-\infty}^{\tau_E} e^{-(t-t')/\tau_\beta} r dt' \right\rangle = \frac{2Np}{\sqrt{2Np}},$$

where the symbol $D\langle x \rangle$ denotes the variance of $x$. In the above we have used the approximations, $\sum_m f(t_m^\alpha) \approx \int_{-\infty}^{\tau_E} f(t') r(t') dt'$, and $\sum_j \sum_m f(t_m^\beta) \approx \int_{-\infty}^{\tau_E} f(t') r(t') dt'$, with $f(t_m^\alpha) = e^{-(t-t_m^\alpha)/\tau_\alpha}$ under the assumption that neurons fire irreversibly and independently.

Combining with the external inputs, the dynamics of a single neuron in Network 1 is written as

$$\tau \frac{dv_i}{dt} = (\mu + r\tau_s) + \sigma \xi_i,$$

where $v_i$ is the membrane potential of neuron $i$, $\sigma$ is the standard deviation of the input noise, $\tau$ is the membrane time constant, and $\xi_i$ is a white noise process with zero mean and variance $\sigma^2$.

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 Network 1, the stationary distributions of membrane potentials of the excitatory and inhibitory neurons pools satisfy the same distribution as in Eq. (17), except that the shape parameters $\beta_E$ and $\beta_I$ are changed accordingly, which are

$$
\beta_E = \frac{\sigma^2 + 0.5(j_E)^2r_E\tau_E,\tau_1,\tau_s + 0.5(j_I)^2r_I\tau_I,\tau_s}{\mu + \sqrt{K_E}r_E\tau_E,\tau_1,\tau_s + \sqrt{K_I}r_I\tau_I,\tau_s},
$$

$$
\beta_I = \frac{(j_E)^2r_E\tau_E,\tau_1,\tau_s + (j_I)^2r_I\tau_I,\tau_s}{2\sqrt{K_E}r_E\tau_E,\tau_1,\tau_s + 2\sqrt{K_I}r_I\tau_I,\tau_s}.
$$

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

$$
r_E = \frac{\sigma^2 + 0.5(j_E)^2r_E\tau_E,\tau_1,\tau_s + 0.5(j_I)^2r_I\tau_I,\tau_s}{2\theta_1^2},
$$

$$
r_I = \frac{0.5(j_E)^2r_E\tau_E,\tau_1,\tau_s + 0.5(j_I)^2r_I\tau_I,\tau_s}{2\theta_1^2} \frac{\partial p_1(u)}{\partial u} |_{\theta_1}
$$

By the self-consistent condition, we have

$$
r_E = \frac{\theta_1\tau_I - \theta_1\sqrt{K_I}r_I\tau_1,\tau_s}{\theta_1^2\tau_E,\tau_1,\tau_s - \theta_1\tau_J\sqrt{K_E}r_E,\tau_1,\tau_s},
$$

$$
r_I = \frac{\theta_1\tau_E,\tau_1,\tau_s - \theta_1\tau_E,\tau_1,\tau_s - \theta_1\tau_J\sqrt{K_E}r_E,\tau_1,\tau_s}{\theta_1^2\tau_E,\tau_1,\tau_s - \theta_1\tau_J\sqrt{K_E}r_E,\tau_1,\tau_s}.
$$

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 stimulus-dependent, we get

$$
\beta_E = \frac{(j_E)^2\theta_1\tau_E,\tau_1 - (j_E)^2\tau_E,\tau_1,\tau_s\sqrt{K_I} + (j_I)^2\tau_E,\tau_1,\tau_s\sqrt{K_I}}{2\theta_1^2\tau_E,\tau_1,\tau_s - 2\theta_1\sqrt{K_I}r_I,\tau_E}
$$

$$
+ \frac{\theta_1^2\tau_E,\tau_1,\tau_s - \theta_1\tau_E,\tau_1,\tau_s - \theta_1\tau_J\sqrt{K_E}r_E,\tau_1,\tau_s}{\theta_1^2\tau_E,\tau_1,\tau_s - \theta_1\tau_J\sqrt{K_E}r_E,\tau_1,\tau_s}.
$$

Both $\beta_E$ and $\beta_I$ are independent of the mean of the external input, which suggest that the stationary membrane potential distribution is insensitive to external input.

4. Conditions for fast tracking

4.1. A simple encoding paradigm

We argue that the strategies used by a neural system to read out information should be computationally simple and can be easily implemented in neural circuits. To implement a simple decoding algorithm, the key is that external stimuli are encoded by simple statistical features of neural activities. It is known that stochastic noises tend to linearize the input–output curve of individual neurons (Trappenberg, 2002). In the above two network models, we have shown by mean-field approximation that the mean of external inputs is linearly encoded by the firing rate of the network when the network is at a stationary state. This result is confirmed by numerical simulations (see Fig. 2(a) and (b)). If the stimulus information is contained in the mean of neuronal inputs (such as the firing rates of retina ganglion cells encodes light intensities), then a neural system can read out this information by simply
counting the number of spikes of the network in a short-time window.

We further check whether the linear encoding scheme holds when the biologically more plausible HH model is used. The result is shown in Fig. 2(d), where the input–output curve deviates from a perfect linear relationship, as have been reported in experimental data (Gustafsson & Wigstrom, 1981; Lacaille & Williams, 1990). However, for a wide range of input values, the linear encoding holds approximately.

4.2. An appropriate noisy structure

In the paradigm of using noise to speed up computation, individual neurons fire irregularly, and it is the statistical property of the transient dynamics of a network that conveys the stimulus information. However, the transient dynamics of a network can be sensitive to its initial state, the structure of noise and the network topology. To achieve fast computation, it is important that the transient dynamics of a network exhibits statistical features which are robust to input fluctuations. Interestingly, we find that when the noise strength is proportional to the mean of inputs, the stationary distribution of neuronal membrane potentials is rather insensitive to the mean of external inputs. This is a very important property, which implies that under the change of external stimuli, the network need not to ‘adjust’ its stationary states in order to catch up the stimulus change quickly. We will confirm this property by simulation in Section 5.

4.3. Impact of network topology

The network topology is another factor that affects the speed of neural computation. In terms of tracking an abrupt change in external inputs, recurrent interactions tend to delay the network response, since the transmission of signals between neurons delays the network to reach a stable state. For the stimulus-dependent noise and the linear IF model, when there is no recurrent interaction between neurons, the tracking speed of the network can be infinitely fast, provided the network size is sufficiently large. When recurrent interactions exist, the tracking delay is mainly due to the transmission delay in recurrent interactions.

5. Tracking time-varying stimuli

In this section, we carry out simulations to confirm our theoretical analysis. To evaluate the speed of network response, we consider a computational task in which the networks track time-varying stimuli. Two scenarios are explored: (1) external stimuli experience an abrupt change, and (2) external stimuli change continuously with time. We measure the response speed of the networks for catching up these changes.

5.1. Tracking an abrupt change in stimuli

In the simulation experiment, the mean of external stimulus is initially set to be \( \mu_{\text{before}} \), and after the network reaching a stable state, we change \( \mu_{\text{before}} \) to be \( \mu_{\text{after}} \) abruptly. The linear IF neuron is used. Fig. 3 shows the network response to this change over time. The firing rate of the network is calculated by counting the number of spikes in a short time-window \( \tau \) (note that the firing rate is highly fluctuated due to the finite size of the network). Denote \( r_{\text{before}} \) and \( r_{\text{after}} \) the firing rates of the network at stationary states before and after the change (they are calculated by the mean firing rates of the network in stationary states). We fit the network response by
Fig. 4. Performances of the network tracking time-varying stimuli. For the stimulus-independent noise, $\sigma^2 = 0.05$. For the stimulus-dependent noise, $\alpha = 1$. The other parameters are: $A = 0.04$, $C = 0.01$, $T = 20$. To have a clear illustration of the tracking process, we have scaled the stimulus values $\mu(t)$ by a constant to match the network response.

Table 1
The reaction times of the network with different input noise forms. The linear IF neuron is used.

<table>
<thead>
<tr>
<th></th>
<th>Stimulus-independent noise</th>
<th>Stimulus-dependent noise</th>
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<tbody>
<tr>
<td>Network 1</td>
<td>4.29</td>
<td>0.34</td>
</tr>
<tr>
<td>Network 2</td>
<td>2.72</td>
<td>0.43</td>
</tr>
</tbody>
</table>

$$r(t) = (r_{\text{before}} - r_{\text{after}}) \exp \left( \frac{t - t_0}{\tau_{\text{react}}} \right) + r_{\text{after}}, \quad t \geq t_0, \quad (39)$$

where $t_0$ is the moment of the stimulus change, and $\tau_{\text{react}}$ the reaction time of the network. The value of $\tau_{\text{react}}$ is optimized by minimizing the square error between $r(t)$ and its actual value. Table 1 summarizes the reaction times of the network with varying structures and noise forms.

We see that for both recurrent structures, the network with the stimulus-dependent noise catches up the stimulus change much quicker than that with the stimulus-independent one, agreeing with our theoretical analysis.

5.2. Tracking moving stimuli

In the experiment, we consider the mean of external inputs changes continuously over time. In particular, we choose the mean has the cosine form, i.e., $\mu(t) = A(1 - \cos(2\pi t/T)) + C$, where the period $T$ determines the changing speed of stimuli, $A$ and $C$ are constants. The linear IF neuron is used. We measure the network firing rates at different moments and fit them with another cosine function with the same period, i.e., $r(t) = A'(1 - \cos(2\pi t/T + \phi)) + C'$. The phase $\phi$, which typically has a negative value, reflects the amount of delay in tracking. Apparently, the closer the value of $\phi$ to zero, the better the tracking performance is. Fig. 4 shows the typical tracking performances of the networks in different noise structures. The corresponding values of phase lag are summarized in Table 2. We see that the phase lag for the stimulus-dependent noise is much smaller than that for the stimulus-independent one, confirming our theoretical analysis.

Table 2
The phase lag of the network in tracking time-varying stimuli. The linear IF neuron is used.

<table>
<thead>
<tr>
<th></th>
<th>Stimulus-independent noise</th>
<th>Stimulus-dependent noise</th>
</tr>
</thead>
<tbody>
<tr>
<td>Network 1</td>
<td>0.676</td>
<td>0.039</td>
</tr>
<tr>
<td>Network 2</td>
<td>0.61</td>
<td>0.01</td>
</tr>
</tbody>
</table>

5.3. Impact of recurrent interactions

We explore the effect of recurrent interactions on the tracking speed of the networks. We choose $w_{ij} = s/Np$ in Network 1 (see Eq. (3)), where the value of $s$ controls the strength of recurrent interactions. Fig. 5 shows the relationship between the phase lag $|\phi|$ and the interaction strength $s$. We see that for both noise structures, the stronger the interaction strength, the larger the phase lag. This result indicates that recurrent interactions tend to delay the network tracking. Furthermore, we see that the phase lag for the stimulus-independent noise is much larger than that for the stimulus-dependent noise.
The period of the stimulus change $T = 20$.

5.4. Trackable speeds

We explore the tracking performances of the network when the speed of the external stimuli varies. Fig. 6 shows the relationship between the magnitude of the phase lag and the speed of the stimulus (measured by $1/T$). We see that the phase lag increases with the speed of the stimulus (i.e., decreasing with $T$). When the speed of the stimulus is too large, the size of phase lag increases dramatically, and the network loses the track of stimuli. This is understandable, since the maximum speed of the stimulus a network can track is restricted by the transmission delay due to recurrent interactions. Furthermore, as expected, the phase lag for the stimulus-independent noise is much larger than that for the stimulus-dependent one.

5.5. Tracking performances with HH neurons

To further check whether our results are applicable to biologically more plausible cases, we use the HH model to describe the dynamics of single neurons, and test the network performances in the above two tracking tasks. The results are shown in Fig. 7 and Table 3. We find that stimulus-dependent noise indeed speeds up network computation, although the improvement is not as significant as in the model of linear IF. We guess this is due to the effects of the leakage term and action potential generation in the HH model. Further study is required to clarify this issue.

6. Discussions and conclusions

In the present study, we have assumed that the stimulus information is carried by the mean of external inputs. To speed up computation, we consider the strength of noise is correlated with the mean of inputs, i.e., the stimulus-dependent noise. Silberberg, Bethge, Markram, Pawelzik, and Tsodyks (2004) proposed a different mechanism to accelerate computation which assumes that the stimulus information is encoded in the variance of external inputs, i.e., $\sigma(t)$. Their idea is that when stimuli change very fast, the potential distribution $p(v, t)$ is almost invariant in a short-time window, but the network response $r(t)$ can catch up the instant changes in $\sigma$ (see Eq. (19)). It is not clear yet which encoding algorithm is more biologically plausible, or they may be used in different computational tasks. Encoding by the mean of external inputs is a traditional view and has been widely observed in sensory or cortical neurons. It dates back to the pioneering work of Adrian and Zotterman (1926) who showed that the firing rate of stretch receptor neurons in the muscles is related to the force applied to the muscle. On the other hand, there are also experimental results showing that neocortical neurons in vivo fire irregularly (Softky & Koch, 1993) and in an apparently irreproducible manner (Schiller, Finlay, & Volman, 1976; Vogels, Spileers, & Orban, 1989), in which cases the mean of inputs is small, suggesting signaling by variance is also possible in cortical areas. We test this scheme of encoding by variance in the tracking task we consider. Fig. 8(a) shows the result when external stimuli experience an abrupt change. We see that the network indeed responds quickly to the stimulus change, and then gradually relaxes to the stationary state, showing an adaptive behavior. In the task of tracking time-varying stimuli (see Fig. 8(b)), interestingly we find that the network response is not phase-lagging, but instead phase-leading. The biological implications of these interesting behaviors are not clear to us.

In summary, the present study investigates the role of stochastic noise in accelerating neural computation. We consider a computational task in which a network tracks time-varying stimuli. Theoretical analysis and simulation results both show that the stimulus-dependent noise, rather than the stimulus-independent one, has better effect on accelerating network computation. This is due to two desirable properties in the transient dynamics of a network: (1) the instantaneous firing rate of the network at a stationary state is proportional to the mean of external inputs, and (2) the stationary state of the network is insensitive to the stimulus change. The first property simplifies the neural encoding/decoding process, and the second one ensures that the equilibrium state of the network serves to be the optimal initial condition for fast computation. We also explore the impact of recurrent interactions on the tracking speed, and find that recurrent interaction tends to delay the network tracking.

Acknowledgment

We acknowledge helpful discussions with Misha Tsodyks. This study is supported by the 973 program of China (grant number 2011CBA00406).

<table>
<thead>
<tr>
<th>Table 3</th>
<th>Tracking performances of the network with HH neurons. Network 1 is used.</th>
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<tbody>
<tr>
<td></td>
<td>Stimulus-independent noise</td>
</tr>
<tr>
<td>$t_{react}$</td>
<td>32.92 ms</td>
</tr>
<tr>
<td>$</td>
<td>\phi</td>
</tr>
</tbody>
</table>
(a) Network 1 with HH neuron and stimulus-independent noise.

(b) Network 1 with HH neuron and stimulus-dependent noise.

(c) Network 1 with HH neuron and stimulus-independent noise.

(d) Network 1 with HH neuron and stimulus-dependent noise.

Fig. 7. (a–b) The network tracking an abrupt change in stimuli; the mean of the external stimulus $\mu(t)$ changes from $\mu_{\text{before}} = 0.1$ to $\mu_{\text{after}} = 0.2$ abruptly at $t_0$. The parameters are: $\alpha = 2$, $t_0 = 80\, \text{ms}$, $\sigma^2 = 0.2$ for the stimulus-independent noise; (c–d) the network tracking time-varying stimuli. For the stimulus-independent noise, $\sigma^2 = 1.2$. For the stimulus-dependent noise, $\alpha = 2$. The other parameters are: $A = 0.5$, $C = 0.1$, $T = 50\, \text{ms}$ Network 1 is used and it contains 1000 neurons.

(a) Tracking an abrupt change in stimuli.

(b) Tracking moving stimuli.

Fig. 8. The tracking performances of Encoding by Variance. The mean of the external inputs is set to be a constant: $\mu(t) = 0.05$. The strength of noise changes with time. In (a), $\sigma^2$ changes from 0.05 to 0.1 instantaneously at the moment of $t_0 = 40$; in (b) $\sigma(t) = 0.01 + 0.04(1 - \cos(2\pi t/T))$, $T = 20$, phase-leading value $|\phi| = 0.424$.

References


