Effect of inhibitory feedback on correlated firing of spiking neural network

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Abstract Understanding the properties and mechanisms that generate different forms of correlation is critical for determining their role in cortical processing. Researches on retina, visual cortex, sensory cortex, and computational model have suggested that fast correlation with high temporal precision appears consistent with common input, and correlation on a slow time scale likely involves feedback. Based on feedback spiking neural network model, we investigate the role of inhibitory feedback in shaping correlations on a time scale of 100 ms. Notably, the relationship between the correlation coefficient and inhibitory feedback strength is non-monotonic. Further, computational simulations show how firing rate and oscillatory activity form the basis of the mechanisms underlying this relationship. When the mean firing rate holds unvaried, the correlation coefficient increases monotonically with inhibitory feedback, but the correlation coefficient keeps decreasing when the network has no oscillatory activity. Our findings reveal that two opposing effects of the inhibitory feedback on the firing activity of the network contribute to the non-monotonic relationship between the correlation coefficient and the strength of the inhibitory feedback. The inhibitory feedback affects the correlated firing activity by modulating the intensity and regularity of the spike trains. Finally, the non-monotonic relationship is replicated with varying transmission delay and different

spatial network structure, demonstrating the universality of the results.

Keywords Correlation coefficient · Oscillation · Feedback · Spectral coherence

Introduction

The fluctuations of correlated response among simultaneously recorded neurons have been recorded in a large number of cortical areas (Akerberg and Chacron 2010; Tchumatchenko et al. 2010a, b; Smith and Kohn 2008; Qu et al. 2012; Li et al. 2011). How correlations of population responses are shaped in neural systems remains unclear. It has been observed, both in experimental systems and in computational models of varying complexity, that the correlations within a population of neurons are influenced by the magnitude and correlations of the external stimuli (Tetzlaff et al. 2008; Lindner et al. 2005). Pairwise correlations in feed-forward circuits generally increase with firing rate (Tetzlaff et al. 2008). This is so when input correlations are not too strong, otherwise the correlations become independent of firing rate (Tchumatchenko et al. 2010). Ostojic et al. (2009) studied the relationship between the synaptic connections and the correlations of the spike trains, and pointed out that common synaptic input could enhance the correlations of neural firing activity. Further, recent work stated that feed-forward inhibitory circuitry could help to prevent excessive correlations in the face of sensory-evoked activation leading to improved population coding (Middleton et al. 2012). These researches have however mainly focused on correlations in isolated neurons or feed-forward inhibitory networks, without involving the feedback loop.

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It is generally known that inhibition can control neural activity in cortex (Wang et al. 2012; Trappenberg 2008). As shown by the experiments of neurophysiology, the inhibitory interneurons could assist in phase-locking postsynaptic neurons in primary visual cortex (Lytton and Sejnowski 1991; Murphy and Rieke 2008; Bartos et al. 2007; Tanji et al. 2005; Marinazzo et al. 2007). Therefore, the feedback input provided by these inhibitory interneurons plays an important role in the correlated activity of preceding neural populations. Especially, gamma oscillations, thought to be fundamental for transmitting information, rely on inhibitory interneurons, and arise from oscillatory, synchronized firing of these interneurons onto pyramidal cells (Bartos et al. 2007; Borgers and Kopell 2003; Brunel and Wang 2003; Mazzoni et al. 2008; Wang and Buzsaki 1996). In the electrosensory system, inhibition is linked to oscillations via global delayed inhibitory feedback (Lindner et al. 2005; Marinazzo et al. 2007; Doiron et al. 2003, 2004), which will be our focus here. By using numerical simulations of a spiking neural network of noise leaky integrate-and-fire (LIF) neurons with delayed inhibitory feedback under the influence of partially correlated input, we obtain the curves of intensity of oscillation, mean firing rate and correlation coefficient with the increase of feedback strength. This model, directly inspired by studies of the lateral line lobe of electric, possesses detailed spatio-temporal correlations, and provides insight into the structure of the neural activity (Lindner et al. 2005; Doiron et al. 2003, 2004; Maler 2007). To further explicate how inhibitory feedback circuit modulates correlations, computational simulations that increase G while concomitantly increasing the bias to maintain a constant firing rate or increasing the external noise to destroy the network oscillations are employed. Finally, we investigate the influences of the transmission delay and network structure on the relationship between correlations and inhibitory feedback. The results suggest that network correlations are affected by inhibitory feedback via the co-variation of mean firing rate and oscillations.

Model and numerical methods

The feedback spiking neural network model is composed of LIF neurons. A population of N excitatory LIF neurons provides excitatory input to a set of M inhibitory LIF neurons. The output of these inhibitory LIF provides inhibitory feedback to the excitatory LIF neurons. Here, $N = 4M$. The proportion is obtained according to the fact that there are about four times more excitatory than inhibitory neurons in large portions of the cortex.

The input to the population of excitatory LIF neurons consists the following components,

$$I_n(t) = \mu_E + \sigma \left[\sqrt{1 - c} \xi_n(t) + \sqrt{c} \xi_c(t) \right] + I_g, \quad (1)$$

where $n = 1, \dots, N$, μ_E is the constant base current. $S_n = \sigma \left[\sqrt{1 - c} \xi_n(t) + \sqrt{c} \xi_c(t) \right]$ represents the external noise with intensity σ , and consists of two noise processes: $\xi_i(t)$ is the individual noise component, and $\xi_c(t)$ is the shared component. They are scaled by the input correlation coefficient c to determine the degree of shared input of all the excitatory neurons: identical external stimulus is associated with $c = 1$, whereas $c = 0$ means the excitatory neurons have no shared external noise. The last term in Eq. (1) denotes the common negative feedback generated by inhibitory neurons, which is calculated by the convolution of a delayed α function and the sum of the spike trains of the inhibitory neurons,

$$I_g = -G \int_{\tau_D}^{\infty} \frac{t - \tau_D}{\tau_I^2} \exp \left[-\frac{t - \tau_D}{\tau_I} \right] \sum_{m=1}^M y_m(t - \tau_D) d\tau, \quad (2)$$

where τ_D and τ_I are the transmission delay of the feedback loop and the time constant of synaptic responses respectively. G is the feedback strength, which is set to be positive, but with a negative sign in Eq. (3) to model the inhibitory interactions of the feedback loop. Just like the excitatory neurons, the inhibitory neurons are induced by all the excitatory neurons with a constant base current, an excitatory feed-forward input given by the convolution of the output of the excitatory neurons and a delayed α function,

$$I_m = \mu_I + \int_{\tau_D}^{\infty} \frac{t}{\tau_E^2} \exp \left[-\frac{t}{\tau_E} \right] \sum_{n=1}^N y_n(t - \tau) d\tau, \quad (3)$$

where $m = 1, \dots, M$, τ_E is the synaptic time constant of feed-forward loop. The output of the LIF neurons is a δ spike train determined by the instants of the action potential of membrane potential,

$$y(t) = \sum_s \delta(t - t_s). \quad (4)$$

The correlation coefficient of the feedback spiking neural network can be estimated by analyzing the temporal properties of the spike trains of the excitatory neurons. The cross-correlogram (CCG) of spike trains of two excitatory neurons i and j (De La Rocha et al. 2007; Kohn and Smith 2005),

$$C_{ij}(\tau) = \frac{\sum_{k=1}^K \sum_{t=0}^L y_i^k(t) y_j^k(t + \tau)}{K(L - |\tau|) \sqrt{\lambda_i \lambda_j}}, \quad (5)$$

where K is the number of trials or realizations, L is the duration of every trial, λ_i and λ_j are the mean firing rates of excitatory neurons i and j , respectively. In Eq. (5), $|L - \tau|$

corrects for the degree of overlap of the two spike trains of excitatory neurons i and j for each time lag. The autocorrelogram (ACG) of the excitatory neurons are calculated similarly as the CCG, but the spike train on each trial is compared with itself by letting $i = j$,

$$C_{jj}(\tau) = \frac{\sum_{k=1}^K \sum_{t=0}^L y_j^k(t) y_j^k(t + \tau)}{K(L - |\tau|) \sqrt{\bar{\lambda}_j \bar{\lambda}_j}}. \quad (6)$$

In the model simulations, $K = 100$ realizations of spike trains with time duration $L = 11$ s are carried out for every group of parameter values by stimulated repeatedly. The first 1 s of each trial is removed to avoid the influence of the initial transient response. The pairwise spike correlation of every two excitatory neurons is estimated by the ratio of the area of the CCG to the geometric mean area of the ACG within a certain range of lags defining a integral time window T :

$$R_{ij}(T) = \frac{\sum_{\tau=-T}^T C_{ij}(\tau)}{\sqrt{\sum_{\tau=-T}^T C_{ii}(\tau) \sum_{\tau=-T}^T C_{jj}(\tau)}}. \quad (7)$$

When T is large enough, R_{ij} saturates to a steady value ρ_{ij} with minimal statistical error (De La Rocha et al. 2007). ρ_{ij} is defined as the pairwise correlation coefficient of excitatory neurons i and j . Here, the correlated firing activity is measured over 100 ms by letting the integral time window $T = 100$ ms. Finally, the correlation coefficient on hundreds of milliseconds time scale of the network is obtained by averaging the pairwise correlation coefficient over all pairs of excitatory neurons,

$$\rho = \frac{1}{N(N-1)/2} \sum_{i=1}^N \sum_{j=i+1}^N \rho_{ij}. \quad (8)$$

The mean firing rate of the feedback spiking neural network describes the intensity of the activity of neurons which is given by averaging K realizations of spike trains of N excitatory neurons,

$$\bar{\lambda} = \sum_{n=1}^N \sum_{k=1}^K \frac{NS_{n,k}}{L}, \quad (9)$$

where $NS_{n,k}$ is the number of the spikes on K realization of neuron n .

The oscillatory activity of feedback spiking neural network is measured by calculating the spike train power spectrum. Since the statistics of spike trains are the same for all excitatory neurons, it suffices to show the power spectrum for neuron i to study the oscillatory activity of the network.

$$S(\omega) = \langle \tilde{y}_i(\omega) \tilde{y}_i^*(\omega) \rangle, \quad (10)$$

and

$$\tilde{y}_i(\omega) = \frac{1}{\sqrt{L}} \int_0^L e^{-i\omega t} y_i(t) dt, \quad (11)$$

where $\tilde{y}_i(\omega)$ is the Fourier transform of the spike train $y_i(t)$, and $\tilde{y}_i^*(\omega)$ denotes the complex conjugate of $\tilde{y}_i(\omega)$. The brackets in Eq. (10) represent an average over multiple realizations of the spike trains of the excitatory neurons induced repeatedly by the external input, which changes from trial to trial. A peak can be seen in the power spectrum at finite frequency for the oscillatory neurons. Therefore, the intensity of the oscillations is quantified by the degree of the coherence with the parameters of the peak in the power spectrum (Lindner et al. 2002),

$$\Gamma_{\omega_1, \omega_2} = \frac{1}{\Delta\omega} \int_{\omega_1}^{\omega_2} S(\omega) d\omega, \quad (12)$$

where $\Delta\omega = \omega_2 - \omega_1$, ω_1 and ω_2 are lower limit and upper limit, respectively, to calculate the integral of the power spectrum. $\Gamma_{\omega_1, \omega_2}$ is the area under the curve of the power spectrum within a certain range of frequency, which measures the peak of the power spectrum. Coherence, used commonly in the field of stochastic nonlinear dynamics, could quantify the sharpness of the peak in the spike train power spectral density (Lindner et al. 2002; Pakdaman et al. 2001).

Correlated activity

For $\mu_E < v_T$, the neurons fire only in the presence of external input. This is referred to as the sub-threshold regime. We focus on the sub-threshold regime to study the influence of inhibitory feedback on the correlated activity of the network. Figure 1 presents the interspike interval, the raster plots, and the spike train power spectrum for one randomly chosen neuron, when $G = 0.1$, $G = 0.3$, $G = 0.7$ respectively. The probability of interspike intervals falling into the different bins, expressed as the count, is plotted against interspike interval. As the inhibitory feedback strength increases, the plot shows a clear progression from spike trains with little structure to network oscillations, and the neurons fires more phase locked to this oscillation. The values of parameters are: $N = 80$, $M = 20$, $\mu_E = \mu_I = 0.9$, $\sigma = 0.2$, $c = 0.2$, $\tau_D = 4$ ms, $\tau_E = 2$ ms, $\tau_I = 10$ ms, $\omega_1 = 40$ Hz, $\omega_2 = 50$ Hz.

The structure of the CCGs at different values of inhibitory feedback strength is showed in Fig. 2. Remarkably, a peak appears around lag zero, which increases with feedback strength. The increasing peak reflects the raised

pairwise correlations. The delayed inhibitory feedback is responsible for the bumps in the C_{ij} , whose magnitudes increase with G . Moreover, C_{ij} is symmetric, which is expected because each neuron in the network has identical parameters and receives the same inhibitory delayed feedback.

We next explore the relationship between the correlation coefficient of the network and the inhibitory feedback gain. Figure 3 shows that with the increase of the strength of inhibitory feedback G , the coherence of spectral peaks $\Gamma_{\omega_1, \omega_2}$ is increased and the mean firing rate $\bar{\lambda}$ is decreased. Accordingly, the correlation coefficient ρ first drops to a lower level for small values of G , but later rises. The non-monotonic curve thus reveals a minimum correlation coefficient of the network for a moderate value of the inhibitory feedback strength.

When G is weak ($G < 0.25$), ρ decreases with increasing G (Fig. 1c), which resembles the trend of $\bar{\lambda}$ at small G (Fig. 1b). The network has no apparent oscillations when G is weak, and $\Gamma_{\omega_1, \omega_2}$ keeps small (Fig. 1a). Therefore, the drop of ρ at small G is mainly due to the effect of sharp decline of $\bar{\lambda}$, which corresponds to the results of Tetzlaff et al. (2008). However, an increase in G leads to growth in $\Gamma_{\omega_1, \omega_2}$ but only a small change in $\bar{\lambda}$. When G exceeds a threshold value ($G = 0.25$), the relatively flat values of $\bar{\lambda}$ imply that the effect of firing rate on ρ keeps almost invariable. Therefore, ρ is raised due to the increase of $\Gamma_{\omega_1, \omega_2}$, when $G > 0.25$. The induced oscillations are

Fig. 2 Cross-correlogram versus time lag

thought to play an important role in the synchronization of neural populations, which accordingly modulate correlations of the neuron activities. Thus, at higher feedback strength the network oscillation has a more important effect on ρ . Afterwards, $\Gamma_{\omega_1, \omega_2}$ and $\bar{\lambda}$ is almost unchanged with further increases in G ($G > 0.7$). The excitatory neurons fire regularly. Eventually, a stable and relatively high level

Fig. 1 Illustrations of the model behavior

Fig. 3 Firing activity of feedback spiking neural network

of pairwise correlation is maintained over this range. The non-monotonic relationship between the correlation coefficient of the network and the feedback strength can be explained by the interplay between the mean firing rate and the spectral coherence of firing activity caused by the inhibitory feedback connections.

Previous studies focus on the influence of mean firing rate on the correlation coefficient. However, the mean firing rate characterizes the activity of the neurons regardless of randomness or periodicity of the spike train. The power spectrum measures the periodic components of the spike train. The correlation of the spike trains on a millisecond time scale is increased with the emergence of the periodic firing activity, which in turn raises the value of correlation coefficient on a time scale of 100 ms. Therefore, the inhibitory feedback loop of the network is beneficial to both the oscillatory and correlated activities of the network. Nevertheless, the mechanisms underlying the non-monotonic relationship between correlations and inhibitory feedback need further work. We addressed this question by confirming the roles of firing rate and oscillatory activity in shaping the correlation coefficient curve.

Relationship between correlation coefficient and inhibitory feedback strength

To gain more insight into the influence of inhibitory feedback on the correlated firing activity of the network, we have also performed simulations for the case where the

mean firing rate is kept constant and equal to its value in open-loop ($G = 0$) by adjusting the bias upwards as G increased ($\bar{\lambda}_i = \bar{\lambda}_0$ with $i = 0.05, 0.1, \dots, 0.95, 1$, which are the non-zero values of feedback strength). This was done to eliminate the effects of the changes in mean firing rate. Figure 4 plots ρ versus G with constant mean firing rate. Here, $G = 0.05, 0.1, \dots, 0.95, 1$ and the corresponding values of base current are $\mu = [0.9, 0.97, 1.07, 1.11, 1.15, 1.22, 1.25, 1.285, 1.34, 1.37, 1.415, 1.44, 1.478, 1.51, 1.54, 1.575, 1.61, 1.65, 1.72, 1.76, 1.81]$, respectively. All other parameters are the same as in Fig. 1.

As shown in Fig. 4, ρ increases monotonically with G as the mean firing rate is kept constant. Since the intensity of the firing activity denoted by the mean firing rate remains unchanged, the correlation coefficient is only associated with the regularity of the firing activity. The increases in ρ are resulted from the emergence of oscillatory activity in networks with inhibitory feedback, which can also be demonstrated by the conclusion that the curve of ρ with constant mean firing rate (Fig. 4) signals the emergence of network oscillations with increasing G (Fig. 3a). Therefore, raising the feedback strength generates more regular network oscillations, leading to an increase of the network correlation coefficient on a time scale of 100 ms.

More numerical simulations are carried out to further investigate ρ versus G . Letting $c = 0$, the external noise is thus equal to $\xi_n(t)$ with intensity σ . With the increase of G , σ is raised to collapse the network oscillations, which ensures the network has no oscillatory activity over the whole range of the values of G selected in the simulations. The effects of spectral coherence on network correlation coefficient are thus eliminated. Figure 5 shows ρ versus G with increasing σ .

For non-oscillatory network, ρ decreases as G increases. Since the network firing activity has no periodic properties, the intensity of the firing activity is responsible for adjusting the network correlation coefficient. Thus, the reduction in ρ caused by increasing G is lined to firing rate

Fig. 4 Relationship between correlation coefficient and strength of inhibitory feedback in network with constant mean firing rate

Fig. 5 Relationship between correlation coefficient and strength of inhibitory feedback in network without oscillation

drops. In fact, the change in ρ in Fig. 5 parallels very closely the decrease in $\bar{\lambda}$ at roughly the same values of G in Fig. 3b. The decline of mean firing rate leads to reduced correlation coefficient on a time scale of 100 ms, which is also implied by Tetzlaff et al. (2008). Hence, the decline in correlation coefficient results from a similar decrease in mean firing rate caused by enhanced inhibitory feedback.

The network correlations are critically dependent on the value of the transmission of the feedback loop. However, for small delay, no network oscillation would be present (Lindner et al. 2005). Therefore, $\tau_D = 1$ is selected to be the start point for simulations. Correlation coefficient is plotted against inhibitory feedback strength and transmission delay in Fig. 6. With the increase in τ_D , a monotonically increasing degree of ρ is obtained for all values of G . That the correlation coefficient becomes bigger with increasing transmission delay is mainly due to the pronounced oscillation in the network (Lindner et al. 2005). At short delay, no sharp delayed activity, with little effects on neuronal firing, is received by the network due to the effect of the α function. The larger the delay is, the more diminished is the effect of the synapse, thus drastic oscillation is accompanied. Furthermore, Fig. 6 illustrates that the relationship between ρ and G is still non-monotonic. Within the region of the parameter space of transmission delay, inhibitory feedback circuit helps to shape correlations in a non-monotonic way, according to our preliminary studies.

Since the structure of network is involved in modulating the firing activity of the neurons (Vida et al. 2006), we now turn to the effect of varying the spatial structure of the network. Throughout this article, we assume that all excitatory neurons are connected to all inhibitory neuron, and vice versa. Later, we consider a network model with modest sparseness. The probability of the connectivity between excitatory and inhibitory neurons is reduced from 1 to 0.5 (Borgers and Kopell 2003). Therefore, each inhibitory neuron receives input from a random population of excitatory neurons. The expected number of this population is 40. Similarly, each excitatory neuron receives input from a

Fig. 6 Correlation coefficient is plotted against inhibitory feedback strength and transmission delay

Fig. 7 Relationship between correlation coefficient and strength of inhibitory feedback in sparse network

random population of excitatory neurons, with expectation 10. Based on this model, the effects of inhibitory feedback on the correlated activity are investigated as shown in Fig. 7. ρ first decays and then goes up, which saturates for large G , yet preserves its qualitative dependence on G . Altogether, in all scenarios, the relationship between correlation coefficient and inhibitory feedback strength is non-monotonic, suggesting that the two opposing effects of inhibitory feedback shapes the correlations of the feedback network.

Conclusion

The role of the variability of neural activity in neural computation is a topic receiving increasing focus. It is important to understand how neural circuitry, previously considered to dictate trial-averaged phenomena, affects the properties of population activity. Furthermore, it is important to understand how inhibitory feedback contributes to the correlations of neural activity.

It is not surprising that the degree of correlation drops with firing rate (De La Rocha et al. 2007), but also increases with the strength of the coupling between cells controlled by the global feedback. The demonstrated non-monotonic relationship between the network correlation coefficient on a time scale of 100 ms and the inhibitory feedback strength is a preliminary study on the influence of inhibitory feedback on correlations. We further examined how inhibitory feedback coupling shapes the correlated variability between the spiking activities in a feedback network architecture.

We found that this non-monotonic relationship is owing to two opposing effects of inhibitory feedback on the network firing activity. The inhibitory feedback offsets the excitatory input of the network, and the correlation coefficient is declined because of the reduction of the firing rate. However, the inhibitory feedback can induce oscillation, which modulates the activity of the excitatory neurons, leading to an improvement of the correlation coefficient of the network. The correlation coefficient is now determined mainly by the oscillatory strength and less by the mean rate. These opposing effects compete, and at some moderate value of inhibitory feedback strength, one expects a trade-off where both effects play a significant role. And below or beyond that point, one effect is expected to dominate over the other, thereby setting the non-monotonic dependence of correlation on feedback strength. This non-monotonic relationship is further supported by numerical simulations employing changes in transmission delay and network spatial structure. Therefore, inhibitory feedback is beneficial for controlling the timing and probability of action potential generation, as well as for generating correlated activity in cortex.

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