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Dynamic random links enhance diversity-induced coherence in strongly coupled neuronal systems

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Abstract. We investigate the influence of diversity on the temporal regularity of spiking in a ring of coupled model neurons. We find diversity-induced coherence in the spike events, with an optimal amount of parametric heterogeneity at the nodal level yielding the greatest regularity in the spike train. Further, we investigate the system under random spatial connections, where the links are both dynamic and quenched, and in all the cases we observe marked diversity-induced coherence. We quantitatively find the effect of coupling strength and random rewiring probability, on the optimal coherence that can be achieved under diversity. Our results indicate that the largest coherence in the spike events emerge when the coupling strength is high, and when the underlying connections are mostly random and dynamically changing.

Keywords. Diversity; coherence resonance.

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1. Introduction

The constructive role of noise in nonlinear dynamical systems, modelling physical, chemical and biological phenomena, has received sustained interest for the past two decades [1–4]. Its role in signal detection and enhancement, as well as pattern formation is well studied. While research in this field started with low-dimensional systems, the frontier of research has now shifted to spatially extended systems [5]. For instance, array enhanced stochastic resonance (AESR) has been observed, where the response of a locally coupled array of identical oscillators to a periodic signal is enhanced under noise [6]. It was also found that coherence could be induced purely by noise, in the absence of an external signal, and this is termed as array enhanced coherence resonance (AECR) [7]. The constructive effects of noise are also investigated in complex networks [8], such as small-world [9] and scale-free networks [10] which are excellent for modelling interactions among the units of complex biological and sociological systems. For small world networks, stochastic resonance [11] and coherence resonance [12,13] were found due to short-cuts between randomly chosen sites, and this dynamical ordering depended on the coupling strength and rewiring probability. For scale-free networks, stochastic resonance was found for a network of bistable oscillators, where a weak signal was found to be amplified under noise [14]. Also, a scale-free network consisting of bistable overdamped oscillators was studied, and stochastic resonance was observed arising from the inherent degree-inhomogeneity of the network [15]. Further, noise and topology-induced coherence in a two-dimensional map-based neuronal system has been recently reported [16].

Naturally, the elements comprising an extended system may differ from each other [17]. So, many studies have been devoted to the constructive role of disparity in a characteristic parameter of the unit system. For example, it is found that the spatiotemporal chaos in an array of coupled pendulums can be tamed by an optimal magnitude of disorder, induced by disparity in pendulum lengths [18], and a resonance-like behaviour is also found in these systems. Tessone *et al* have found that different sources of diversity, such as those represented by quenched disorder or noise, can induce a resonant collective behaviour in an ensemble of coupled bistable or excitable systems [19]. This phenomenon is termed as diversity-induced resonance. Thus, diversity can play a constructive role analogous to that of the noise. In the context of neuronal systems, diversity-induced coherence resonance was found for a one-dimensional ring of map-based neuron systems [20].

Now in various naturally occurring network topologies, the coupling between the nodes in the network may change over time [21], especially in social and biological networks. It is shown that the rapid switching of random links among chaotic maps enhances spatiotemporal regularity of their dynamics [22–24]. The constructive effects of noise has also been considered for these networks. For example, for diffusively-coupled FitzHugh–Nagumo model neurons, coherence resonance is induced by rewiring [25]. Also, fast random rewiring and strong connectivity are found to impair subthreshold signal detection in excitable networks [26]. In this paper, we aim to study the interplay of dynamic random connections and diversity on coherent behaviour in an extended neuronal system.

Specifically, we consider a coupled ring of heterogeneous neurons, with some fraction of dynamic or static random links. The static random links are invariant throughout the evolution of the system, whereas the dynamic links are switched at time-scales comparable to the nodal dynamics [22]. We shall investigate the effect of both types of random connections on diversity-induced coherence in the firing patterns of the neurons.

Our principal questions are the following: do random links enhance diversity-induced temporal coherence in neuronal networks? Is there any significant distinction in temporal coherence for a network with dynamic (switched) random connections and one where the random links are quenched (or static)? In this work we shall show that the greatest diversity-induced coherence is achieved in a strongly coupled network with dynamic random connections.

This paper is organized as follows. In §2, we shall describe the mathematical model, as well as the order parameter for the system, which measures the temporal regularity in spiking of model neurons in the network. The numerical results are presented in §3. In the last section, we summarize and discuss our findings.

2. Model of coupled neurons with diversity

We consider networks of diffusively-coupled elements with the nodal dynamics given by a map, which was introduced by Rulkov [27]. This map captures all the essential features of neuronal dynamics ranging from regular spiking to self-sustained chaotic bursting. Temporal evolutions of these coupled elements are described by the following sets of equations:

$$\begin{aligned} x_{n+1}(i) &= f_\alpha[x_n(i), x_{n-1}(i), y_n(i) + \beta_n(i)], \\ y_{n+1}(i) &= y_n(i) - \mu(x_n(i) + 1) + \mu\sigma(i), \end{aligned} \tag{1}$$

where $i(=1, \ldots, N)$ is the site index, N is the total number of elements in the lattice and n is the discrete time index. Also, $x_n(i)$ is a fast variable which represents membrane potential and $y_n(i)$ is a slow variable due to the small value of the parameter μ ($\mu = 0.001$). Here $\beta_n(i)$ represents the external input and $f_\alpha(x, x', y + \beta)$ is a piecewise nonlinear function which is designed to shape spiking oscillations in fast subsystems. It contains three intervals which can be described as follows:

$$f(x, x', y + \beta) = \begin{cases} [\alpha/(1 - x)] + y & \text{for } x \leq 0 \text{ and } x' \leq 0, \\ \alpha + y & \text{for } 0 < x < \alpha + y \text{ and } x' \leq 0, \\ -1 & \text{for } x \geq \alpha + y \text{ and } x' > 0. \end{cases}$$

The control parameters of the map are α and σ. In the absence of external input, i.e., for $\beta = 0$, the map generates spikes, if $\sigma > \sigma_{\text{th}} = 2 - \sqrt{\alpha}$, for α less than 4.0, or else it stays in a silent state. For $\alpha > 4$, there are bursts of spikes including both periodic and chaotic bursting. In this work, the value of α is fixed and diversity in the lattice is introduced through the parameter σ. The value of $\sigma(i)$ for the site i is taken from a Gaussian distribution with mean σ_0 and variance D^2. Thus, D measures the diversity in the system. As usual, we study the excitable system in the parameter regime close to a bifurcation point. So, through diversity the system can be pushed above or below the threshold [19].

The external signal, or coupling term, for this network is

$$\beta_n(i) = \frac{\epsilon}{2}[x_n(\xi) + x_n(\eta) - 2x_n(i)], \tag{2}$$

where ϵ is the strength of diffusive coupling. $\xi = (i + 1)$ and $\eta = (i - 1)$ for the nearest-neighbour coupling (with periodic boundary conditions). For random connections, we consider the situation where a fraction, p, of randomly chosen sites in this lattice are coupled to other random sites, instead of their nearest neighbours, i.e., ξ and η are random sites. Clearly, the topology of the network can be changed by adjusting rewiring probability parameter, p. For regular networks (nearest-neighbour coupling), $p = 0$ and for completely random network, $p = 1$. Further, we consider two cases: (i) static random connections, where the random links in the system are quenched and do not change over time; (ii) dynamic random connections where the random links can switch at the time-scale of the local map updates, namely the connectivity matrix changes at each instant n.

The temporal coherence of firing of neurons in the networks is usually measured by the distribution of the pulse interval, $S_k(i)$ [28]. The pulse interval is defined as, $S_k(i) =$

$\tau_{k+1}(i) - \tau_k(i)$, where, $\tau_k(i)$ is the time of the kth spike in the ith neuron. The sharpness of the distribution is given by

$$Z = \frac{\langle S_k(i)\rangle}{\sqrt{\langle [S_k(i)]^2\rangle - [\langle S_k(i)\rangle]^2}} \tag{3}$$

with

$$\langle [S_k(i)]^n\rangle = \frac{\sum_{i=1}^{N}\sum_{k=1}^{k_i}[S_k(i)]^n}{\sum_{i=1}^{N} k_i}$$

which is the ratio of the average and the standard deviations of interspike interval and is a measure of coherence of spike events. Biologically, it is related to the timing precision of information processing [28]. Larger values of Z imply a better temporal regularity of spikes. Also, Z is considered to be zero if all the neurons are in the silent state.

3. Diversity-induced coherence

In this work we investigate the effect of quenched and dynamic random links on the temporal regularity of spiking, under increasing diversity, in a network composed of inhomogeneous neurons. Now, the individual neurons will generate spikes if the value of the parameter $\sigma(i)$ is equal to or greater than the threshold value, $\sigma_{\text{th}} = 2 - \sqrt{\alpha}$. Here, the parameter α of the nodal map is chosen to be 3.0, and so $\sigma_{\text{th}} \sim 0.268$. With no loss of generality, we consider a network of size $N = 500$, and in the network, σ_i of the constituent neurons is randomly distributed about an average value σ_0 with variance D^2, with $\sigma_0 = 0.25 < \sigma_{\text{th}}$. As there are several neurons with $\sigma_i < \sigma_{\text{th}}$, an adequate level of diversity D is necessary in order to enable the active elements in the network to induce spiking behaviour in the subthreshold neurons.

In particular, we study the quantitative measure of temporal coherence Z, with respect to the following important parameters: (a) measure of diversity, D, (b) coupling strength, ϵ and (c) fraction of sites, p, with random (quenched or dynamic) links. Note that the value of Z is obtained by averaging over 100 different initial conditions. For each initial condition, the first 10^5 iterations (transience) are discarded and the subsequent 10^5 iterations are used for calculating Z.

Representative cases of the temporal coherence of neuronal spikes for increasing diversity D, are shown in figures 1–3. In all cases, it is clearly evident that temporal coherence in spiking increases with diversity up to an optimal level of diversity $D = D_{\text{opt}}$, where one attains the maximum coherence $Z_{\max}$. After that, increasing diversity has a detrimental effect on coherence, and increasing D decreases the value of Z. This indicates that a moderate level of diversity is most conducive for temporal coherence in spike events. This diversity-induced coherence holds true in all kinds of coupling topologies, ranging from a one-dimensional ring to networks with varying fractions of quenched and dynamic random links.

Also note that when coupling is weak, regular coupling yields the highest degree of coherence. However, when coupling is strong, larger fraction of random links enhance diversity-induced coherence. Additionally, dynamic random links yield significantly higher levels of temporal coherence than quenched random connections. So, our results

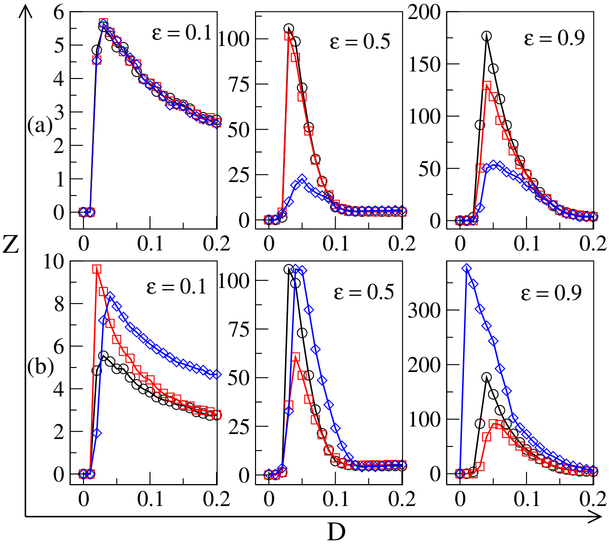

Figure 1. Temporal coherence Z vs. diversity D, for different values of coupling strength ϵ. The black curve represents regular nearest-neighbour coupling ($p = 0$), while the red and blue curves show results from networks with quenched and dynamic random links, respectively, for (**a**) $p = 1/N = 1/500$ and (**b**) $p = 0.9$. The other parameters are $N = 500$, $\alpha = 3.0$ and $\sigma_0 = 0.25$.

demonstrate that the largest coherence in the spike events emerge when the coupling strength is high, and the underlying connections are mostly random and dynamically changing.

Further, figure 2 shows that more diversity is needed for optimal coherence when coupling is stronger. That is, D_{opt} is larger for larger coupling strength ϵ. On the other hand, higher degree of randomness in connection entails that the diversity needed for maximal

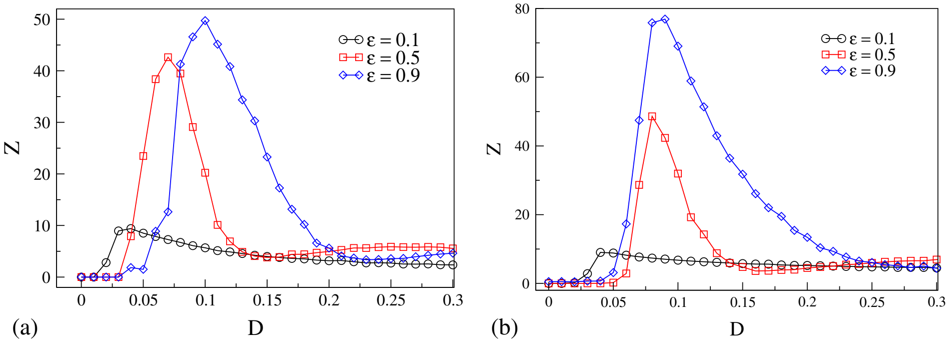

Figure 2. Temporal coherence Z vs. diversity D, for **(a)** quenched random links and **(b)** dynamic random links, for different values of coupling strength ϵ. The rewiring probability $p = 0.5$ for both cases, while the other parameters are $N = 500$, $\alpha = 3.0$ and $\sigma_0 = 0.25$.

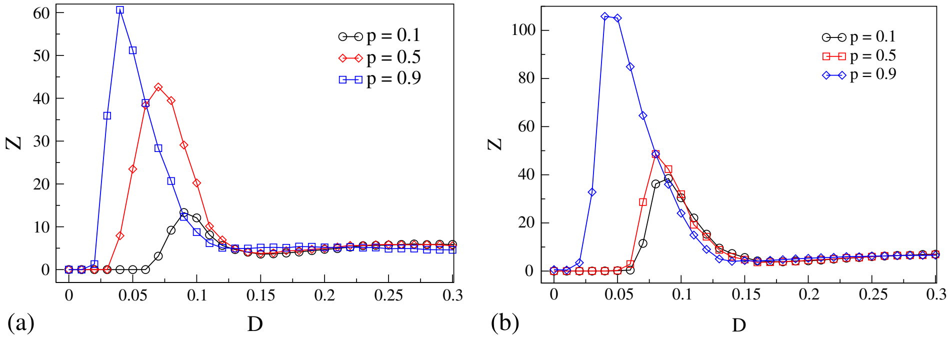

Figure 3. Temporal coherence Z vs. diversity D, for **(a)** quenched random links and **(b)** dynamic random links, for different values of random rewiring probability p. Here, the coupling strength, $\epsilon = 0.5$ for both cases, and the other parameters are $N = 500$, $\alpha = 3.0$ and $\sigma_0 = 0.25$.

coherence is smaller. This is evident from figure 3, which shows decreasing D_{opt} with increasing p.

Now we investigate the value of $Z_{\max}$, averaged over 10^2 realizations, for varying coupling strengths ϵ and fraction of random links p. This quantitatively captures the trends evident in figures 1–3.

The broad trend evident from figures 4 and 5 is that the maximal coherence that can be induced by diversity increases with increasing coupling strength ϵ and increasing degree of randomness in spatial connections. This implies that, for a given level of diversity, in a lattice which has larger degree of random spatial connections, larger coupling strength helps the spiking neurons to induce activity in the silent neurons, thereby enhancing temporal coherence in the system. Furthermore, comparing the values of $Z_{\max}$ clearly shows that dynamic links are significantly more conducive to temporal coherence than quenched random links. Therefore, there is a marked increase in the temporal coherence of spikes in strongly coupled systems, with large number of random links. Specifically, the optimal

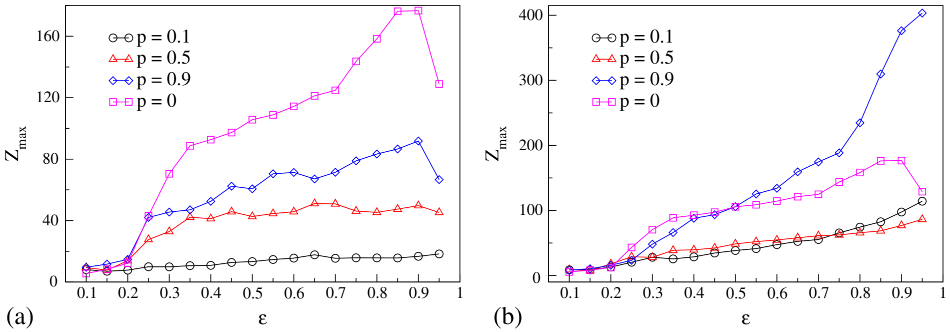

Figure 4. Maximum temporal coherence $Z_{\max}$ (see text) vs. coupling strength ϵ, for **(a)** quenched random links and **(b)** dynamic random links. For $p = 0$ the regular nearest-neighbour coupling is shown in both figures for reference. The other parameters are $N = 500$, $\alpha = 3.0$ and $\sigma_0 = 0.25$.

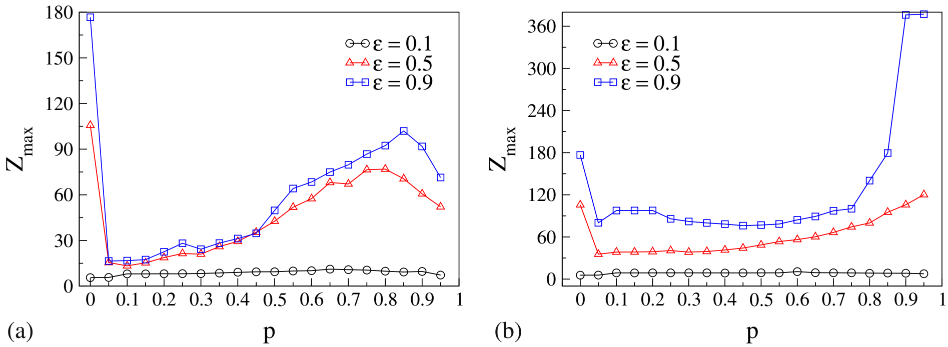

Figure 5. Maximum temporal coherence $Z_{\max}$ (see text) vs. random rewiring probability p, for different values of coupling strength ϵ, for **(a)** quenched random links and **(b)** dynamic random links. The points for $p = 0$ represent the value of $Z_{\max}$ for each ϵ in nearest-neighbour coupling and are included for reference. The other parameters are $N = 500$, $\alpha = 3.0$ and $\sigma_0 = 0.25$.

coherence that can be achieved, i.e., $Z_{\max}$, is quadrupled for dynamic links, compared to quenched connections, for large p and ϵ.

Lastly, for quenched random links, the dependence of the maximum temporal coherence on p, differs from the case of dynamic links for high p. The value of $Z_{\max}$ increases to an optimal value (e.g., $p \sim 0.85$ for $\epsilon = 0.9$, as seen in figure 5a), and then decreases as the value of p increases further. This non-monotonic dependence of $Z_{\max}$ indicates that too many quenched random links actually hinder coherent spiking. This is unlike dynamic links, where increasing the fraction of random links continues to aid coherence.

4. Summary

In conclusion, we investigated the influence of diversity on the temporal regularity of spiking in a ring of coupled model neurons. We found diversity-induced coherence in the spike events, with an optimal amount of parametric heterogeneity at the nodal level yielding the greatest regularity in the spike train. Further, we investigated the system under random spatial connections, where the links were both dynamic and quenched, and in all cases we observed diversity-induced coherence. We quantitatively found the effect of coupling strength and random rewiring probability, on the optimal coherence that could be achieved under diversity. The results indicate that the largest coherence in the spike events emerge when the coupling strength is high, and the underlying connections are mostly random and dynamically changing. Future research directions include the study of continuous time systems and other classes of dynamical networks, such as scale-free networks. Investigations into these open and potentially important problems will shed light on the generality of the phenomena presented here.

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