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Review

Chimera states in neuronal networks: A review

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Abstract

Neuronal networks, similar to many other complex systems, self-organize into fascinating emergent states that are not only visually compelling, but also vital for the proper functioning of the brain. Synchronous spatiotemporal patterns, for example, play an important role in neuronal communication and plasticity, and in various cognitive processes. Recent research has shown that the coexistence of coherent and incoherent states, known as chimera states or simply chimeras, is particularly important and characteristic for neuronal systems. Chimeras have also been linked to the Parkinson's disease, epileptic seizures, and even to schizophrenia. The emergence of this unique collective behavior is due to diverse factors that characterize neuronal dynamics and the functioning of the brain in general, including neural bumps and unihemispheric slow-wave sleep in some aquatic mammals. Since their discovery, chimera states have attracted ample attention of researchers that work at the interface of physics and life sciences. We here review contemporary research dedicated to chimeras in neuronal networks, focusing on the relevance of different synaptic connections, and on the effects of different network structures and coupling setups. We also cover the emergence of different types of chimera states, we highlight their relevance in other related physical and biological systems, and we outline promising research directions for the future, including possibilities for experimental verification.

Keywords: Neuronal networks; Synchronization; Chimeras; Synaptic communication; Multilayer networks

1. Introduction

The human brain is a very challenging complex system [1] where neurons and their interconnections through synapses form possibly the most complicated structure. A simple subdivision of the entire information processing system, i.e. the vertebrate nervous system, consists of the central nervous system and the peripheral nervous system. The peripheral nervous system is made up of the nerves that are situated outside of the brain or the spinal cord. While the central nervous system comprises of the brain and the spinal cord and it is the place where information received by the sense organs are stored and managed. The presence of about 86 billion neurons and thousands times more

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synapse in the nervous system of the human brain has made it so mysterious that its complexity is yet to be resolved. Neurons are comprised of different components, among which the special connection that transfers signals from one neuron to another is known as the synapse [2]. Such connections can usually be found at the dendrites of a neuron and sometimes also directly at the soma. Synapses can be of two types, namely electrical synapse and chemical synapse. Electrical synapse is an electrically conductive link between two neighboring neurons that is formed at the gap junction between two neurons. At a chemical synapse, a neuron discharges neurotransmitter molecules into the synaptic cleft that is adjacent to another neuron. As the distance between synaptic junctions is shorter for electrical impulses, they move faster whereas in case of chemical synapses, the process of sending messages using neurotransmitter is slower. The advantage of electrical synapses is the absence of delay while the advantage of chemical synapses lies in their versatility. Rhythmicity or synchrony among large number of neurons in neuronal ensembles is very much essential for various neurobiological processes, which mainly appears due to the inter-neuronal synaptic interactions.

In general, synchronization [3–5] refers to a dynamical process wherein two (or many) systems adjust a given property of their motion to a common behavior due to interaction between each other or to a forcing. And neuronal networks, among other complex systems, self-organize in such ways that synchronous spatiotemporal patterns can emerge. Synchrony in neuronal networks is required for normal and various cognitive functions, neuronal communication, neural plasticity and in memory processes [6]. Essentially, the ref. [7] explained that the task-related alpha synchronization in frontal brain regions is associated to top-down processing and high internal processing demands.

On the other hand, since the first observance of coexisting coherence and incoherence patterns by Kuramoto and Battogtokh [8] in nonlocally coupled phase oscillators, this captivating phenomenon, popularly known as chimera state [9-11] has been elaborately investigated during the past decade in a wide range of systems. For instance, study of chimera states in phase oscillators includes a number of illustrious articles [8,12–15]. In fact, it has been shown that they are not limited to originate in coupled phase oscillators, but can also be realized in a large variety of different systems including neuronal networks. In chaotic systems [16,17], different types of chimeric patterns are identified. As far as the coupling topology is concerned, these states have been found in globally coupled [18–23] as well as in locally connected [18,24-27] dynamical networks. Chimera states have also been realized in networks having unconventional interactions [28–41]. This covers a broad range of ideas, e.g., study of the ref. [28] revealed that the chimera states are sturdy against perturbations in the form of inhomogeneous elements with regular coupling topology in network of FitzHugh-Nagumo oscillators and also studied networks of identical elements with irregular coupling topologies. Existence of chimera-like states in modular neuronal network based on the idea of the connectome of the C. elegans soil worm in presence of hybrid synapses, is discussed in ref. [29]. Ko et al. [42] studied chimera patterns in the form of partially locked states in a network of identical phase oscillators with scale-free distribution of coupling strength. In ref. [30], authors have investigated properties of chimera states and their dependence on parameters for both scale-free and Erdös-Rényi networks. Presence of stable, breathing, and alternating chimera states in time varying complex networks made of two coupled sub-networks of Kuramoto oscillators, where the links between the two groups are assumed to vary with time, is reported [31]. The robustness of chimera pattern with respect to random removal of links is revealed in [32]. C.R. Laing [43,44] analyzed chimera state in heterogeneous networks for which the natural frequencies of the oscillators are chosen from specific distributions and depending on its form, the heterogeneity is found to affect the chimera states in a diverse way and also the influence of heterogeneous coupling strengths have been discussed. Besides numerical and theoretical studies [45], chimera patterns have been widely inspected in experimental models as well. These include optical coupled-map lattices realized by liquid crystal spatial light modulators [46], populations of coupled chemical oscillators [47], two sub-populations consisting of identical metronomes [48], superconducting squid meta-materials [49], and electronic nonlinear delay oscillators [50]. On the other hand, nonlocality in coupling induces spiral wave chimera states [15,51–55] with a possibility in locally coupled scenario [56] in spatially extended systems, that exhibit phase-randomized spiral core of desynchronized oscillators enclosed by phase-locked dynamical units in the spiral arms.

In this context, we would like to emphasize that recent researches [18,24,25,27–29,33,35,57–62] in dynamical networks substantiate that these patterns are particularly likely to incarnate in a variety of neuronal models, the deliberation of which is the focus of the present review. In fact, potential applications of chimera states in nature incorporate various neural processes, such as the bump states in neural systems in which localized regions of coherent oscillation are surrounded by incoherence and the phenomenon of unihemispheric slow-wave sleep of some birds and aquatic mammals, which sleep with one eye open, suggesting that half of the brain is synchronized with the other half being asynchronous. Besides, this sort of co-existence of synchronization and desynchronization is strongly con-

nected to various types of neuronal diseases [63], namely Parkinson's disease, epileptic seizures, Alzheimer's disease, schizophrenia and brain tumors. For these reasons, it is particularly interesting that such states were recently observed in leaky integrate-and-fire neurons with excitatory coupling, as well as in networks of FitzHugh–Nagumo and Hindmarsh–Rose neuronal oscillatory systems. Chimera-like states have also been analyzed for non-locally coupled Hodgkin–Huxley oscillators and in many other different neuronal network models. Also there exists observational evidence of this concurrent patterns in electrical brain activity. Tognoli et al. [64] reported that during studies where participants were asked to coordinate left and right finger movement with a periodically flashing light, EEGs revealed clusters of coordinated and uncoordinated activity.

Since, chimera state is defined as the coexistence of coherent and incoherent dynamics in a symmetrically coupled identical dynamical units, due to such peculiarity, this new discovery has drawn a lot of attention of many physicists, biologists and applied mathematicians in the last decade. From the above discussion, it is evident that the study of chimera state in neuronal networks deserves special attention in near future as this state is highly relevant from the perspective of various neuronal developments.

We have organized this review in the following way. Section 2 is devoted to the discussion of aptness of the chimera-like patterns in the light of several neuronal evolution with focus on neural bump states, phenomenon of unihemispheric sleep, and some brain diseases. In Section 3, we describe the details of particular models of FitzHugh–Nagumo and Hindmarsh–Rose systems considered for most of the studies on chimera state in the literature. Different types of possible synaptic organizations of a neuronal network are illustrated in Section 4. Section 5 deals with the presentation of general dynamical model of neuronal networks followed by the description of the quantitative measures used in order to differentiate various collective states observed. In Section 6, we concentrate on the materialization of chimera-like patterns based on diverse synaptic organizations of the considered neuronal network, for instance, the presence of only electrical, only chemical and of both types of synapses will be reviewed in details. Through Section 7, we conclude with a summary and future prospects illustrating the challenges ahead in the study of chimera in neuronal systems.

2. Pertinency in light of neuronal evolution

The brain function relies on the inter communication among the neurons. During the interaction among numerous neurons in large neuronal networks, a group of neurons get divided and lumped into highly connected subnetworks. For the coordination or the normal functioning, the interaction follows a mechanism or a class of mechanisms that evolved to coordinate the activity within the sub-ensembles. For a number of neuronal processes, such as visual information processing, sleeping, and memory in the brain [65–67], the neuronal rhythm [68] plays a crucial role. Due to the excitable behavior, neurons emit spikes or bursts [69,70] in the form of electrical signals for governing brain functions. The collective rhythmic behavior of neuronal oscillations may appear in different patterns. In this consequence, the collective oscillatory dynamics may behave in synchrony, remain disordered or exhibit both types of characteristics simultaneously. In the nonlinear dynamics literature such concurrence is termed as "chimera" or "chimera-like" states. Experimental studies on brain function have been done based on measuring electrical activities non-invasively, through the technique of electroencephalography (EEG) and it was revealed that there are several structures of collective neuronal oscillation formed in the brain. The EEG signals exhibit oscillations at different range of frequency that represent various brain functions appearing during a diversity of behavioral states (for example, that associated with different stages of sleep). In the following, we discuss the resemblances of coexistent synchronous and desynchronous dynamics (i.e., "chimera state") from different aspects of neuronal activities.

2.1. Neural bump states

Neurons are excitable units and due to the recurrent excitations, a new type of neural activity appears in the form of pulse or bump which are spatially localized. The bump has been associated with the mechanisms of visual systems, head direction systems and working memory. The bump like neural activity appears in coupled neuronal network of spiking neurons. The chimera or chimera-like states have strong connection to the bump behavior of the neuronal networks. In the bump states, the spatially localized regions consist of partially coherent neuronal oscillations completely incoherent oscillations that mimic chimera-like states. In ref. [71], the front and stationary bumps are studied in both one and two spatial dimensions where the moving fronts connect the regions of high local synchrony (coherent

motion) together with regions of complete asynchrony (disordered or incoherent motion). Laing et al. [72] studied the networks of pulse coupled integrate-and-fire neurons and they revealed that partial synchronizations of the neurons may be the main reason for the termination of bump states. Apart from these investigations, chimera-like state was also reported in the electrical brain activity [64]. Here the experiment was performed while considering the interaction between two hands and the interaction between each hand and visual signals. It was shown that the coupling between the two hands is much stronger than the coupling between the hands and rhythmic environmental signal, which is a resemblance of chimera features in terms of the combination of symmetry (coordination of two hands) and symmetry breaking (coordination of hands and external visual stimulus) situation. From the data analysis, it was revealed that the diluted coordination dynamics composed of the phase locking and metastability, appears at a high frequency. The chimera and chimera-like patterns have also been studied in a few neuronal ensembles, which includes coupled Hodgkin–Huxley oscillators [73], Hindmarsh–Rose model [29,59], FitzHugh–Nagumo oscillators [28,57], discrete Rulkov map [27], leaky integrate-and-fire neurons [60], and in many other neuronal network models where the coupling topology is regular as well as in complex network form [10].

2.2. Unihemispheric sleep

Chimera-like features are strongly related to quite a few neuronal processes, among them 'unihemispheric slowwave sleep' is one of the most prominent behavioral form observed in some aquatic mammals, such as dolphins, eared seals, and manatees [74,75], and some migratory birds [74]. During the slow-wave sleep, these species sleep with half of the brain which means they shut down only one cerebral hemisphere of the brain and close the opposite eye. During this time, the other half of the brain monitors what is going on in the environment (for migratory birds) and controls breathing functions (for aquatic mammals). In this case, the neuronal oscillations in wake part of the cerebral hemisphere is desynchronized while the oscillations in the sleepy part is very much synchronized. In this context, the experimental EEG records show that the sleeping hemisphere exhibit high-amplitude, low-frequency neuronal oscillations while the other hemisphere (awake side) exhibit low-amplitude, high-frequency neuronal electrical activity. The presence of such mixed types of coordination in the hemisphere is a strong indication of the chimeralike feature. The coexistence of coherent and incoherent neuronal oscillations in the hemisphere may be studied as considered in the model [13] where chimera states were observed. Mukhametov et al. [76] experimentally studied the EEG data on dolphins and they revealed that the two brain hemispheres of dolphin could produce synchronized and desynchronized motion not only simultaneously but also generated independently and such activity patterns alternate between the hemispheres over time. In this context, Ma et al. [77] studied two coupled population of Kuramoto phase oscillators to simulate the alternating synchronization behavior and they found that with proper tuning of the interaction strength, the synchronous and desynchronous behavior may alter in each subpopulation. These are the various pieces of evidence of the evolutionary function asserted by unihemispheric sleep, which is characterized on the neurophysiological level by coexistence of coherent and incoherent brain activities.

2.3. Brain disorders

Apart from the previously mentioned scenarios, chimera like anomalous synchronization also resembles certain pathological brain states like Parkinson's disease, Alzheimer's disease, autism, epileptic seizures, schizophrenia etc. Synchronized neuronal responses among large number of neurons are involved in various cognitive and executive processes like perceptual awareness, working memory etc. and also undertakes crucial role in motor-related activities, such as movement preparation and visual-motor coordination [78]. For instance, during Parkinson's disease, an atypical increase in neuronal synchrony in the basal ganglia is observed and one suffers from dysfunctions in motor activity, attention, perception [79,80]. Whereas Alzheimer's disease is related to reduced synchronization of oscillations [81] in the α -, β - frequency band, and also in γ - band in the resting state, that also results in cognitive dysfunctions. Epilepsy refers to peculiar enhancement in local neural synchronization along with reduction in long-range synchrony yielding a number of heterogeneous neurological disorders characterized by seizures [82,83]. Several EEG studies have demonstrated that schizophrenia is also related to damaged local and long-range neural synchronization [84], impairing cognitive abilities.

Thus there are certain aspects that correlate chimera like abnormal synchrony to several neuronal activities and for this reason, study of such exceptional dynamical phenomenon in neuronal systems demands significant deliberation.

3. Neuronal models

Neuronal rhythmicity is realized by diverse dynamical mechanisms that may be analyzed and described through a set of mathematical equations [85]. In order to properly predict certain biological processes which are associated to the neuronal behavior, several mathematical neuronal models were developed. Among them, Hodgkin–Huxley neuron model [86] is widely used for the study of diverse features of neurons, invented by Hodgkin and Huxley based on the data from the squid giant axon. The mathematical description of this model is very complicated and so after a number of modifications and simplifications, similar type of models have been proposed, such as FitzHugh–Nagumo model [87,88] and the Hindmarsh–Rose model [89]. The qualitative local dynamical behaviors including regular bursting, chaotic bursting, rhythmic spiking of neurons can be accurately captured by these two neuronal models. So, for studying various collective dynamical patterns arising in networks of coupled neurons, we consider these two simple paradigmatic models in this review. In the following subsections, we briefly describe some inherent features of isolated FitzHugh–Nagumo and Hindmarsh–Rose models.

3.1. FitzHugh-Nagumo model

The two dimensional FitzHugh–Nagumo model describes the process of activation and deactivation dynamics of a spiking neuron. The mathematical form of the individual system is described by the following set of ordinary differential equations:

$$\epsilon_0 \dot{u} = u - \frac{u^3}{3} - v,$$

$$\dot{v} = u + \mu.$$
(1)

This system exhibits limit cycle relaxation oscillation for proper choice of the excitability threshold μ and u, v represent the activator and inhibitor variables, $\epsilon_0 > 0$ is the parameter characterizing the time scale separation of fast activator and slow inhibitors. Whenever $|\mu| < 1$, the system follows the oscillatory motion while the system is in excitable state if $|\mu| > 1$.

3.2. Hindmarsh-Rose model

The three-dimensional Hindmarsh–Rose neuronal model, which is well known for showing all common dynamical features found in a number of biophysical modeling studies of bursting, in its original form is expressed as follows,

$$\dot{x} = y + ax^2 - x^3 - z + J,
\dot{y} = 1 - dx^2 - y,
\dot{z} = c(b(x - x_0) - z),$$
(2)

where the variable x represents the membrane potential of the neuron, variables y and z are associated to the transport of ions across the membrane through the fast (e.g., sodium) and slow (e.g., potassium) channels respectively. J is the magnitude of stimulus current that enters the neuron and c corresponds to the inverse of a time constant, determines how fast z changes and x_0 is a control parameter delaying and advancing the activation of the slow current in the modeled neuron. As a simplification, we employ a linear transformation $x \longrightarrow x$, $y \longrightarrow 1 - y$, $z \longrightarrow 1 + J + z$, $d \longrightarrow a + \alpha$, $e \longrightarrow -1 - J - bx_0$ so that the above equations become

$$\dot{x} = ax^2 - x^3 - y - z,
\dot{y} = (a + \alpha)x^2 - y,
\dot{z} = c(bx - z + e).$$
(3)

Small values of c lead to slow evolution of z compared to the variables x and y. Particularly choosing a = 2.8, $\alpha = 1.6$, c = 0.001, b = 9, and e = 5, square wave bursting can be witnessed in the above model.

4. Neuronal synaptic communication

Information transformation among neurons mainly happen through two types of functional connections, one is chemical synapse and the other one is electrical gap junctional communication. The signals are carried chemically

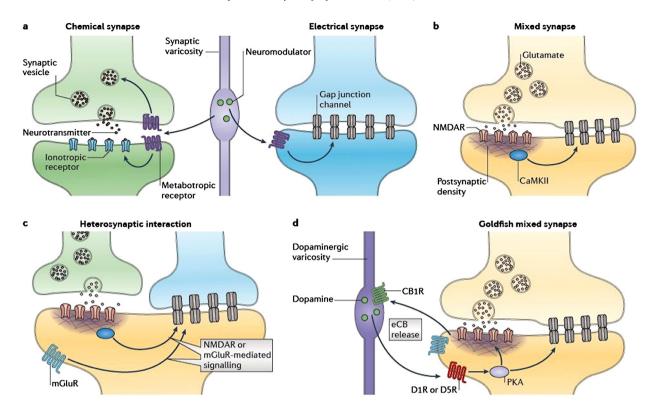


Fig. 1. Different types of neuronal interactions through electrical and chemical synapses in the nervous system. (a) Chemical transmission occurring through chemical synapses and electrical transmission mediated via gap junction between two neurons. (b) Mixed synaptic interaction: simultaneous electric and chemical synaptic interactions between two neurons. (c) Heterosynaptic interaction: one neuron interacts with two other neurons simultaneously, one connected through the gap junction channel and the other through chemical synapse. (d) The mechanism of mixed synaptic interaction of goldfish. Figure reproduced with permission from [2].

through the chemical synapses via neurotransmitter molecules such as gamma-Aminobutyric acid, Acetylcholine, dopamine and serotonin, packaged within the small synaptic vesicles. In a stochastic way, exocytosis releases the neurotransmitters from a pre-synaptic neuron into the adjacent synaptic cleft. After that, these molecules are detected and bind to specific post-synaptic receptors in adjacent neuronal cells. In such unidirectional transmission of information process, the distance between pre- and post-synaptic ends is approximately 20-40 nm [90]. In case of electrical synapses, the cytoplasm of the adjacent cells is directly connected by intercellular channels called gap junction. Within the pre-synaptic end and the post-synaptic neuron, electric current, cyclic AMP, calcium and inositol-1,4,5 trisphosphate transmission occurs bidirectionally. In this case, the membranes of pre- and post-synaptic neurons are very close to each other, approximately 3.5 nm [91]. In most of the nervous systems, these two types of synapses are present simultaneously. But the inter neuronal synaptic communication may not necessarily occur simultaneously via these two types of synapses, rather they perform independently [2]. When two neurons interact through both electrical and chemical synapses then this neuronal communication is known as mixed synaptic communication while in case of hetero synaptic interaction, one neuron communicates with two other neurons in such a way that one is connected through chemical synapses and the other one interacts via electrical gap junction. For a better understanding, different types of possible modes of synaptic communication are shown in Fig. 1. Fig. 1(a) describes the interactions between two neurons which occur independently through either electrical or chemical synapses, while Figs. 1(b) and 1(d) represent the interaction in presence of both synapses. A single neuron interacts with other two neurons among which one is connected through electrical synapse and other one through chemical synapse, the corresponding schematic diagram is shown in Fig. 1(c).

A large neuronal network gets divided into subnetworks at the time of interaction among the neurons and the communications happen through different types of synapses within the subnetworks where the underlying network topology may be regular or irregular. In Section 6, we study the existence of chimera states in regular types of network

topology which includes local (nearest neighbor), global (all-to-all), nonlocal and also other possible network structures such as multilayer networks, small world network while considering identical neuronal oscillators to cast the local dynamical units. Time delay in the synaptic communications is inevitable due to finite signal transmission speed from one neuron to another. So the study on the time delay effect in coupling function on chimera states in neuronal networks is very crucial. In the Section 6, we have discussed the role of synaptic delay on chimera states.

5. General dynamical equation for neuronal communication

Here we present the general mathematical framework for a neuronal network consisting of N identical neuronal oscillators. Each node of the network represents a d- dimensional dynamical system and the corresponding state vector of the i-th node is denoted by $X_i = (x_{i,1}, x_{i,2}, ..., x_{i,d})^T$ and whose local dynamics is governed by the flow $F(X_i)$. The coupling between the i-th and j-th neuron is denoted by the function $H(X_i, X_j) \in \mathbb{C}^1$. The dynamical equation of the entire network is then described as

$$\dot{X}_i = F(X_i) + K_e \sum_{i=1}^N A_{ij}(e) D_e H_e(X_i, X_j) + K_c \sum_{i=1}^N A_{ij}(c) D_c H_c(X_i, X_j), \tag{4}$$

where $A_{ij}(e,c)$ represents the adjacency matrices determining the connectivity between i-th and j-th neurons for electrical and chemical synaptic interaction functions $H_{e,c}(X_i,X_j)$ with coupling strengths K_e and K_c respectively. Here $D_{e,c}$ are the appropriate $d\times d$ diagonal matrices corresponding to electrical and chemical synapses respectively. The general form of the electrical coupling between the i-th and j-th neurons is of linear diffusive type (i.e., $H_e(X_i,X_j)=X_j-X_i$) while the chemical synaptic function is a non-linear sigmoidal function, represented by $H_c(X_i,X_j)=(v_s-X_i)\Gamma(X_j)$ where $\Gamma(x)=\frac{1}{1+e^{-\lambda(x-\Theta_s)}}$. In the following subsections, we discuss the functions of three quantitative measures, namely strength of inco-

In the following subsections, we discuss the functions of three quantitative measures, namely strength of incoherence and discontinuity measure, mean phase velocity and local order parameter which are used to characterize the chimera states together with incoherent and coherent dynamics. In order to compute these measures, long time averages of each oscillatory dynamics in the network are considered.

5.1. Strength of incoherence and the discontinuity measure

To distinguish the disordered (incoherent), chimera, multi-chimera and coherent states, we use the statistical measures, named as strength of incoherence and discontinuity measure following a local standard deviation analysis [92]. The computations of strength of incoherence and discontinuity measure are based on the time series of the each dynamical unit in the network. To calculate these statistical measures, we first introduce transformations $w_{l,i} = x_{l,i} - x_{l,i+1}, l = 1, 2, ..., d, i = 1, 2, ..., N$ and divide the number of oscillators into M (even) bins of equal length n = N/M. Then the local standard deviation is defined as

$$\sigma_l(m) = \left\langle \sqrt{\frac{1}{n} \sum_{j=n(m-1)+1}^{mn} [w_{l,j} - \langle w_l \rangle]^2} \right\rangle_t, \tag{5}$$

where m = 1, 2, ..., M and l = 1, 2, ..., d; i = 1, 2, ..., N, and $\langle w_l \rangle = \frac{1}{N} \sum_{i=1}^{N} w_{l,i}(t)$ and $\langle \cdot \cdot \cdot \rangle_t$ denotes the average over time. The above quantity $\sigma_l(m)$ can be calculated for every successive n number of oscillators. Then the strength of incoherence is defined as,

$$SI = 1 - \frac{\sum_{m=1}^{M} s_m}{M}, \ s_m = \Theta(\delta_0 - \sigma_l(m)),$$
 (6)

where $\Theta(\cdot)$ is the Heaviside step function and δ_0 is a predefined threshold. Consequently, the values of SI=1, SI=0 and 0 < SI < 1 represent disordered, coherent and chimera or multi-chimera states respectively. Again in order to distinguish chimera from multi-chimera states, we also introduce the so called discontinuity measure which is defined as

$$DM = \frac{\sum_{i=1}^{M} |s_{i+1} - s_i|}{2}, \text{ with } s_{M+1} = s_1.$$
 (7)

For chimera state the value of DM = 1 and for multi-chimera state the value of DM is a positive integer greater than "1" and $2 \le DM \le \frac{M}{2}$.

5.2. Mean phase velocity

To verify the existence of chimera states together with incoherent and coherent states in coupled systems, we compute the long time averaged mean phase velocity of each neuron defined [57] as

$$\omega_i = \frac{2\pi M_i}{\Lambda T}, i = 1, 2, ..., N, \tag{8}$$

where M_i is the number of spikes of the *i*th neuron during a sufficiently long time interval ΔT . The values of ω_i have random distribution for incoherent states and are constant for coherent states. For chimera and multichimera states, ω_i lie on a continuous curve and only the intervals of constant ω_i correspond to the coherent regions where neighboring elements are phase locked.

5.3. Local order parameter

The notion of *local order parameter* (LOP) is used to characterize the coherent–incoherent patterns and chimera state. The local order parameter actually signifies the local ordering of the neurons reflecting the degree of coherence and incoherence, and is defined [24,57] as

$$L_i = \left| \frac{1}{2\nu} \sum_{|i-k| \le \nu} e^{j\Phi_k} \right|, i = 1, 2, ..., N,$$
(9)

where $j = \sqrt{-1}$ and ν is the number of nearest neighbors on both sides (of a ring) for the i-th neuron and Φ_i is the geometric phase of the i-th unit. The local order parameter of the i-th neuron, $L_i \approx 1$ ensures that the i-th neuron belongs to the coherent population of the chimera state, i.e., $L_i = 1$ represents the maximum ordering or coherency. On the other hand, $L_i \approx 0$ indicates that the i-th neuron belongs to the group of incoherent neighboring neurons.

6. Coexistence of coherent and incoherent patterns in coupled neurons under different synaptic communication

In this section, we discuss the incarnation of different collective dynamics, mainly emphasizing on the appearance of chimera states in coupled neuronal networks. Different possibilities of synaptic communications such as solely electrical, chemical and heterosynaptic interactions are considered in the excitatory and inhibitory regimes on top of diverse network topologies.

6.1. Chimera states via electrical synapses

We initiate our proceeding with the exploration of the influence of only electrical synapses in the coupled neuronal network. This type of neuronal interaction is shown earlier in the right panel of Fig. 1(a). Number of studies have been done investigating collective dynamics, such as oscillation suppression, synchronization etc. in the sole presence of electrical synapse in two coupled as well as network of neuronal oscillators. Chimera state is a symmetry breaking situation that appears in symmetrically coupled network of identical oscillators. So, here we will be discussing three types of regular networks, namely local, nonlocal and global topologies. It has been shown that using only electrical synapse, complete neural synchrony appear merely in globally coupled networks for which the information get exchanged at a time among all the neurons in the ensemble, otherwise the oscillators are phase locked under the local interaction. It has been demonstrated that the chimera state is possible only when the regular coupling topology is in nonlocal format. Taking only electrical synapse in nonlocally coupled neuronal network, chimera states are observed in Hindmarsh–Rose [59] and FitzHugh–Nagumo models [57]. The FitzHugh–Nagumo system is a paradigmatic model for excitable behavior, particularly for exhibiting spiking dynamics in neurons and it has a wide range of application from biological processes to optoelectronic oscillators and nonlinear electronic circuits. Now, we consider

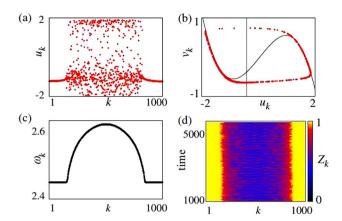


Fig. 2. Chimera states in nonlocally coupled FitzHugh–Nagumo model. (a) The snapshots of the activator variable u_k with respect to number of node and (b) the phase space where black represents the nullcline of the FitzHugh–Nagumo systems. (c) and (d) correspond to the mean phase velocity ω_k and local order parameter Z_k . The other parameters are fixed at N=1000, $\mu_k=\mu=0.5$, R=0.35, $\sigma=0.1$, $\epsilon_0=0.05$, $\gamma=D=0$ and $\phi=\pi/2-0.1$. Here u_k , v_k , ω_k and Z_k bear the same connotations as u_i , v_i , ω_i and L_i in Eqs. (10), (8), (9). Figure reproduced with permission from [57].

the neuronal network of N nonlocally coupled FitzHugh–Nagumo oscillators in presence of noise and time delayed feedback coupling function. The corresponding dynamical equation is given by,

$$\epsilon_{0}\dot{u}_{i} = u_{i} - \frac{u_{i}^{3}}{3} - v_{i} + \frac{\sigma}{2P} \sum_{j=i-P}^{i+P} [b_{uu}(u_{j} - u_{i}) + b_{uv}(v_{j} - v_{i})] + \gamma \epsilon (u_{i}(t) - u_{i}(t - \tau))$$

$$\dot{v}_{i} = u_{i} + \mu_{i} + \frac{\sigma}{2P} \sum_{j=i-P}^{i+P} [b_{vu}(u_{j} - u_{i}) + b_{vv}(v_{j} - v_{i})] + \sqrt{2D} \xi_{i}(t),$$
(10)

where u_i and v_i are the activator and inhibitor variables of the i-the oscillator respectively, for i=1,...,N,N is the total number of the neuronal oscillators in the network. ϵ_0 is defined as a time-scale separation parameter and for $|\mu_i| < 1$, the individual FitzHugh–Nagumo oscillator is in oscillatory regime in which the system has unstable steady state while for the excitable state $|\mu_i| > 1$. σ is the over all effective coupling strength and P is the number of nearest neighbors in each direction of the ring with respect to the i-th neuron and parameter $R = \frac{P}{N}$ is the coupling radius. γ and τ represent the self feedback strength and delay time. Also, $\xi_i(t)$ denotes the Gaussian white noise with intensity P and P and P are P are P and P are P and P are P and P are P are P and P are P are P and P are P and P are P are P and P are P are P and P are P and P are P and P are P and P are P are P and P are P are P and P are P and P are P and P are P are P are P and P are P are P and P are P are P and P are P are P are P and P are P and P are P are P are P and P are P and P are P and P are P are P and P are P are P are P are P and P are P are P and P are P are P and P are P and P are P and P are P a

$$C = \begin{pmatrix} b_{uu} & b_{uv} \\ b_{vu} & b_{vv} \end{pmatrix} = \begin{pmatrix} \cos \phi & \sin \phi \\ -\sin \phi & \cos \phi \end{pmatrix},$$

which depends on a single parameter $\phi \in [-\pi, \pi)$.

Emergence and existence of chimera states in nonlocally coupled FitzHugh–Nagumo neuronal oscillators in absence of time delay feedback and noise, are shown in Fig. 2, where u_k , v_k , ω_k and Z_k (for k=1,2,...,N) bears the same meaning as the variables u_i , v_i , ω_i and L_i (for i=1,2,...,N). The snapshot of the amplitude of u_k at a particular instant is plotted in Fig. 2(a). The incoherent population of the chimera state is scattered along the limit cycle whereas the coherent domain follows a smooth profile as illustrated in Fig. 2(b) where the black line denotes the nullcline of the FitzHugh–Nagumo model. The mean phase velocity ω_k and local order parameter Z_k are plotted respectively in Figs. 2(c) and 2(d) corresponding to the chimera profile observed in the Fig. 2(a). The robustness of the chimera state is also studied in the coupled FitzHugh–Nagumo systems in ref. [28]. Here authors investigated how this chimera state changes with respect to the induced heterogeneity in the local dynamics as well as in the network structure. It was commonly believed that chimera states can only appear in symmetrically coupled network with identical node. To overcome this limitation, they considered networks of nonidentical units with regular coupling

topology, and networks of homogeneous elements with irregular interaction topologies. They demonstrated that the chimera states are robust with respect to small heterogeneity in a symmetric nonlocal configuration with nonidentical oscillators and if inhomogeneity is increased the multiple incoherent regions get converted to a chimera state with a single incoherent region. On the other hand, random structural perturbation does not affect emergence of chimera states in a network of identical oscillators and even chimera states can be realized under the addition of large number of random links. These findings may be important in view of experiments as well as from application perspectives, since in real world situation, it is very difficult to find absolute identical units and also complex interaction topologies are rather common in nature. In this context, Hizanidis et al. [59] also investigated the emergence of chimera states in nonlocally coupled two and three dimensional Hindmarsh–Rose neuronal models and consequently they identified the existence of mixed oscillatory states where the desynchronized neurons were interspersed among either stationary or synchronized neurons.

Very recently, emergence of chimera states and other complex spatiotemporal patterns are studied in brain networks [93], where the network architecture consists of two types of connectivity such as, empirical structural brain network configuration and a simulated modular fractal topology. They simulated the epileptic seizures and enunciated that the proper tuning of the coupling parameter leads to initiation or termination of pathological synchrony that happens through chimera states. Correspondingly, they discussed synchronizability of the neuronal network against removal of nodes.

6.1.1. Chimera states via noisy electrical synapses

Noise are omnipresent in nature as well as in neuronal systems. Under the impact of noise, the emergence of chimera states were investigated in nonlocally coupled excitable systems in presence of electrical synapse [94]. Here noise plays a constructive role for the temporal motion of the chimera states in a network of identical units. The combination of temporal behavior of coherence resonance and the spatial properties of chimeras produced a Coherence-Resonance chimera state that corresponds to an alternating periodic spatial switching of the incoherent and coherent domains which is different from the classical chimera state observed in deterministic oscillatory systems. In presence of Gaussian white noise, the applicable coupled neuronal network is presented in Eq. (10). In absence of the time delayed feedback (i.e., $\gamma = 0.0$), four different regimes were observed depending on the respective values of the noise intensity D, as in Fig. 3, where the variation in spatiotemporal motions are described by the variables u_i and local order parameter Z_i , shown in extreme left and middle columns respectively. The extreme right column of the figure depicts the snapshots of Z_i for different time instants. For lower values of the noise intensity (D < 0.000062), the entire network possesses the homogeneous steady state dynamics (cf. Fig. 3(a)) and for intermediate values of D (0.000062 $\leq D \leq$ 0.000325), coherence resonance chimera states were observed. Slightly increased values of D > 0.000325 destroy such chimera patterns and the ensemble becomes incoherent in space but periodic in time. Further increasing the noise intensity to D = 0.1 (strong intensity) induced incoherent dynamics both in space and time.

6.1.2. Chimera states via delayed electrical synapses

Noise induced coherence resonance chimera state has also been investigated under the impact of time delayed feedback coupling in the network of nonlocally coupled FitzHugh–Nagumo oscillators. In ref. [95], authors articulated the controlling mechanism of such type of chimera patterns and they showed that the chimera region may get enlarged or shrinked with proper tuning of the delayed feedback strength. The shifts among different dynamical regimes, namely synchronization, steady state, spatially incoherent spiking and coherence resonance chimera were mapped against the noise intensity and systems' parameter in presence of time delayed coupling.

6.2. Chimera states via chemical synapses

Here we will be discussing how a network of neurons interacting through chemical synapses may develop such intriguing chimera patterns. As far as the influence of network configuration is concerned, we will initiate our discussion with the simplest interaction scenarios of regular topologies.

First we discuss the remarkable finding of chimera and multichimera states in networks of bursting Hindmarsh–Rose oscillators under local, non-local and global coupling architectures. Let us now consider a neuronal network of Hindmarsh–Rose systems with nonlocal interaction topology as the following:

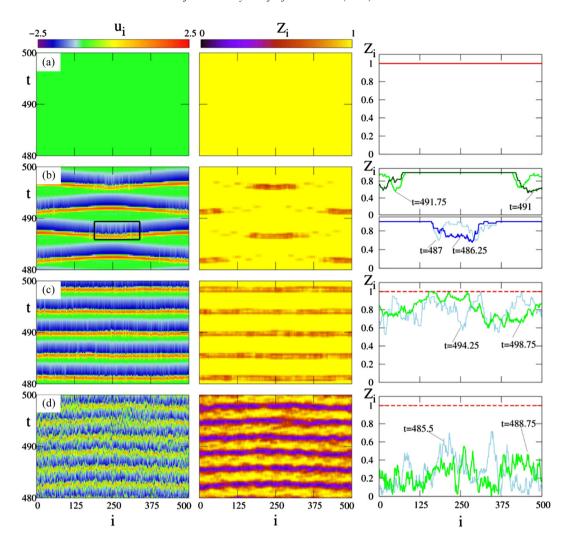


Fig. 3. Left and middle columns represent the spatiotemporal behavior of the state variable u_i and local order parameter Z_i respectively. The right column denotes the variation of Z_i against i for particular time instants: (a) steady state behavior for D=0; (b) coherence-resonance chimera whenever D=0.0002. The black rectangle stands for the incoherent domain. (c) spatial incoherence but periodic nature in time for D=0.0004; (d) incoherent in both space and time with D=0.1. The other parameters are $\epsilon_0=0.05$, $\mu_i=\mu=1.001$, $\sigma=0.4$ and R=0.12 and $\gamma=0$. Here Z_i bears the same connotation as L_i in Eq. (9). Figure reproduced with permission from [94].

$$\dot{x}_{i} = ax_{i}^{2} - x_{i}^{3} - y_{i} - z_{i} + \frac{\epsilon}{2P}(v_{s} - x_{i}) \sum_{j=i-P}^{i+P} c_{ij} \Gamma(x_{j}(t - \tau))$$

$$\dot{y}_{i} = (a + \alpha)x_{i}^{2} - y_{i}$$

$$\dot{z}_{i} = c(bx_{i} - z_{i} + e), \qquad i = 1, 2, ..., N$$
(11)

N being the total number of neurons in the network and P the number of coupled nearest neighbors in each direction on a ring with $R = \frac{P}{N}$ as the coupling radius. Here ϵ is the chemical synaptic strength that connects the neurons in such a way that if i-th and j-th neurons are connected, then $c_{ij} = 1$, otherwise $c_{ij} = 0$ with $c_{ii} = 0$. The parameter τ is the time-delay required to propagate the information from j-th neuron to the i-th neuron. In neuronal networks, the time-delay in signal transmission between different units is inevitable and it may genuinely arise because of the reaction times at chemical synapses. The chemical synaptic coupling function $\Gamma(x)$ is described by the sigmoidal nonlinear input—output function as

$$\Gamma(x) = \frac{1}{1 + e^{-\lambda(x - \Theta_s)}},\tag{12}$$

with λ defining the slope of the function and Θ_s is the synaptic threshold.

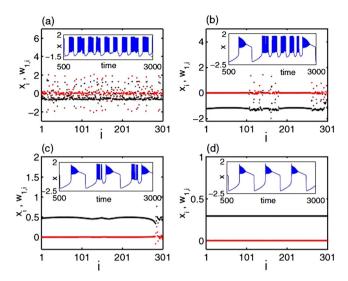


Fig. 4. Snapshots of membrane potentials x_i (black color) and the transformed variables $w_{1,i} = x_i - x_{i+1}$ (red color) for different values of the chemical synaptic coupling strength ϵ characterizing: (a) incoherent state for $\epsilon = 1.0$; (b) chimera state (with two synchronized and desynchronized domains) for $\epsilon = 1.2$; (c) chimera state (with single incoherent group) for $\epsilon = 1.28$; and (d) coherent state for $\epsilon = 1.3$. The insets show the corresponding time evolutions of the neurons. Here N = 301. Figure reproduced with permission from [18]. (For interpretation of the colors in the figure(s), the reader is referred to the web version of this article.)

The coupling range P controls the topology of the interactional structure, from local (nearest neighbor) to global (all-to-all) through nonlocal. Initially, we shall discuss the existence of chimera states in absence of the chemical synaptic delay τ . The authors in ref. [18] have demonstrated the emergence of chimera states for all possible values of P (even for local and global cases) quite elaborately. With $P = \frac{N-1}{2}$ corresponding to the global interaction, the snapshot of the membrane potentials x_i and of the transformed variables defined as $w_{1,i} = x_i - x_{i+1}$ are depicted in black and red dotted points, respectively in Fig. 4. The difference variable $w_{1,i}$ actually defines a local coherence between two neighboring neurons in such a way that if the two neurons oscillate synchronously then $w_{1,i} \to 0$ and $w_{1,i}$ obtains non-zero value if the neurons oscillate incoherently. For a comparatively lower chemical synaptic coupling strength $\epsilon = 1.0$, the network possesses incoherent (disordered) state, as in Fig. 4(a) with the inset showing square-wave nature of time-evolution of the neurons. Fig. 4(b) shows snapshots for x_i and $w_{1,i}$ representing chimera pattern (with two incoherent domains) due to an increment in the synaptic strength $\epsilon = 1.2$. Mixture of square-wave and plateau bursting is realized in all the neurons (cf. inset of Fig. 4(b)). Further increase in ϵ to $\epsilon = 1.28$ leads the network experiencing chimera state having a single incoherent group of neurons, as shown in Fig. 4(c) with the inset showing coexistence of square-wave and plateau bursting, as before. For even higher $\epsilon = 1.30$, Fig. 4(d) explains that the neurons follow plateau bursting dynamics and remain in coherent state. Here it is observed that increasing values of the chemical synaptic strength induce mixed type of bursting dynamics from a square wave bursting state for which the network exhibits multichimera and chimera states. For higher synaptic strength the neurons start following plateau bursting dynamics and consequently the network realizes coherent state.

The ref. [18] revealed that even when the neurons interact locally through chemical synapses without any timedelay τ , the network may experience chimera patterns, unlike the case when only electrical synapses are the communicating medium among the neurons. Next we will be investigating what influence the chemical synaptic delay τ has on the evolution of the neuronal network with local (nearest neighbor) interaction.

In order to get a complete perception of the effect of τ on the dynamical behaviors of the network, the authors of ref. [25] rigorously plotted the two parameter phase diagram in the $\tau - \epsilon$ plane for N = 200 locally coupled Hindmarsh–Rose neurons, as in Fig. 5. Here strength of incoherence is used as color bar in Fig. 5(a) to distinguish different dynamical states, namely incoherent, chimera and coherent states. Further to characterize chimera and multichimera states separately, we plot the $\tau - \epsilon$ plane in terms of discontinuity measure, shown in Fig. 5(b). Fig. 5(a) illustrates that whenever the delay τ is small, for increasing ϵ the network realizes chimera patterns (0 < SI < 1) mediating the incoherent (SI = 1) and coherent states (SI = 0) within the range $\epsilon \in [0, 4]$. But interestingly, as τ exceeds

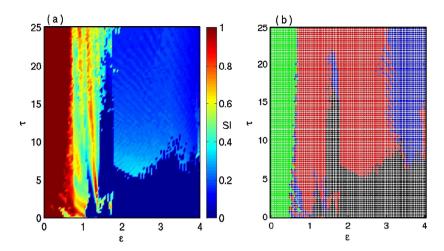


Fig. 5. Two-parameter phase diagram in $\tau - \epsilon$ plane for N = 200 locally coupled Hindmarsh–Rose neurons. (a) Strength of incoherence is used in color bar to discriminate incoherent, chimera and coherent states; (b) The discontinuity measure is used to distinguish between chimera and multichimera states. Here M = 40 and $\delta_0 = 0.05$. Figure reproduced with permission from [25].

some certain value, the network does not reflect coherence any more for any of the considered values of ϵ . Moreover, the values of discontinuity measure in Fig. 5(b) confirms this in which green color indicates incoherent states, black represents coherent states, red for multichimera and blue is for chimera states.

Depending on the spatio-temporal motions of the neurons in the network, different type of chimera patterns have been observed. For instance, a novel dynamical phenomenon named *imperfect traveling chimera state* emerged due to local, synaptic *gradient* coupling in an ensemble of neurons following Hindmarsh–Rose bursting dynamics [24]. While the neuronal network goes through this dynamical state, the chimeric pattern travels over time in the spatio-temporal domain. However, this travel is a bit erratic, as some neurons belonging to the synchronized domain enters into the traveling incoherent domain. Before going into the details, let us have a look at the network model:

$$\dot{x}_{i} = ax_{i}^{2} - x_{i}^{3} - y_{i} - z_{i} + (v_{s} - x_{i})[(\epsilon + r)\Gamma(x_{i+1}) + (\epsilon - r)\Gamma(x_{i-1})],$$

$$\dot{y}_{i} = (a + \alpha)x_{i}^{2} - y_{i},$$

$$\dot{z}_{i} = c(bx_{i} - z_{i} + e), \qquad i = 1, 2, ..., N(\geq 3).$$
The network parameters have the same meaning as before. In addition to them, here r accounts for the strength of

All the network parameters have the same meaning as before. In addition to them, here r accounts for the strength of gradient coupling. Considering the typical case of $\epsilon > r$, one can see that the i-th neuron is connected to the (i+1)-th neuron with synaptic interaction strength $\epsilon + r > 0$ and connected to the (i-1)-th neuron with synaptic coupling strength $\epsilon - r > 0$, $i = 1, 2, \cdots N$. Thus all the neurons are coupled to their nearest neighbors through asymmetric excitatory synaptic interactions.

With a fixed value of the gradient coupling strength r=0.2 and small $\epsilon \lesssim 0.5$, the neuronal ensemble undergoes through an incoherent (disordered) state. However for higher ϵ , the network starts experiencing a peculiar dynamical pattern of chimera state in which coherence and incoherence simultaneously appear but much more interestingly the chimeric patterns travel over time in the spatiotemporal domain. Meanwhile, some neurons from the coherent domain join the traveling incoherent domain and thus the incoherent population expands to the coherent population signifying that the observed pattern does not resemble the pure traveling chimera state, rather indicates the emergence of a novel imperfect traveling chimera state. The manifestation of such a state is explained in Fig. 6. The spatiotemporal evolution of the membrane potentials x_i , $(i=1,2,\cdots,N)$ of all the neurons in the network are depicted in Fig. 6(a) for $\epsilon=0.7$ and r=0.2 which shows that the chimera patterns are traveling in space and time $t \in [1000, 6000]$. The spatial concurrence of coherent and incoherent states are discernible from the snapshot of the membrane potentials x_i in Fig. 6(b). In pursuance of characterizing the chimera state, the local order parameters L_i (cf. Eq. (9)) are plotted in Fig. 6(c). The red region corresponds to the synchronized domain while the desynchronized domain is represented in blue. As can be seen, the width of the incoherent domain varies as it travels in the space and the incoherent domain expands which evidences the emergence of imperfect traveling chimera state. The plateau bursting mode of the individual neurons during this chimeric evo-

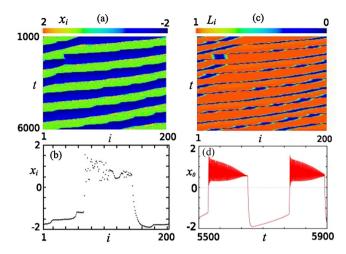


Fig. 6. Imperfect traveling chimera state in a Hindmarsh–Rose neuronal network under asymmetric excitatory local coupling with $\epsilon > r$: (a) Spatiotemporal plot whenever $\epsilon = 0.7$ and r = 0.2. (b) Snapshot of the membrane potentials x_i at time t = 2000. Local order parameters L_i with respect to neuron indices i. Red color represents coherent and blue signifies incoherent domains. (d) Time evolution of a particular neuron in the ensemble. Here N = 200. Figure reproduced with permission from [24].

lution is shown in Fig. 6(d). In the ref. [24], authors also discussed the other possible cases of one way local synaptic gradient coupling ($\epsilon = r$) and simultaneous effect of the excitatory and inhibitory chemical interactions ($\epsilon < r$). They found imperfect chimera in a very narrow region of the ($\epsilon - r$) plane and the transition to the traveling chimera took place in the $\epsilon < r$ region. The time evolution of each neuron was also highlighted in this context.

The emergence of chimera-like states were investigated in a neuronal network model of cat brain [96] as well. The cerebral cortex of the cat can be divided in 65 cortical areas which are organized into the four cognitive regions like visual, auditory, somatosensorymotor and frontolimbic. The local dynamics of each system was modeled through Hindmarsh–Rose neuronal oscillators. Depending on the connectivity matrix of the cat cerebral cortex, authors found two types chimera-like states such as spiking chimera-like states where spikes are in and bursting chimera-like state where bursts exhibit desynchronized dynamics. In addition, they also studied the existence of chimera-like states in the network under the influence of noise. For lower noise intensities, no significant change on the chimera-like states was identified but for stronger noise intensities, chimera-like states got suppressed and the neuronal network experienced neuronal network experienced desynchronized neuronal dynamics. They further concluded that the more robust than the spiking chimera-like states under noisy impacts in the neuronal network.

6.3. Chimeras via electrical and chemical synapses

Next we move on to review the notable appearances of chimera states in neuronal networks in the presence of both electrical and chemical synaptic interactions. In order to perfectly model a neuronal network, focusing on any single type of connecting synapse may come at the expense of ignoring the other, because a structural neuronal network consists of connections from both electrical and chemical synapses.

To start with, we concentrate on the work regarding the emergence of chimera-like states in neuronal network proposed in the ref. [29] based on the nervous system of the nematode Caenorhabditis elegans (C. elegans) soil worm. Recently, lot of attention has been paid to the exploration of the nervous system of C. elegans and small-world topology [97–101] over a modular architecture has been identified. Particularly, a network organized in six communities, found through a community detection algorithm (walktrap method) is considered in [29]. Again, since the extent over which chemical synaptic function is much larger than that of the electrical synapses, so the electrical and chemical synapses are respectively presumed to operate within and across the communities. The network model is thus described in terms of the Hindmarsh–Rose local dynamics (cf. Eq. (2)) as the following:

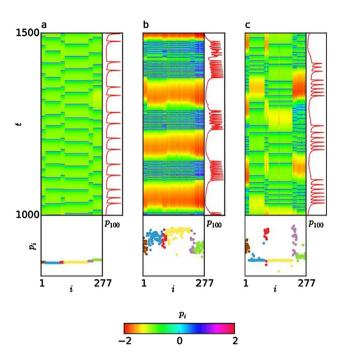


Fig. 7. The spatiotemporal dynamics of the membrane potentials p_i (in left) together with the time series p_{100} for a particular neuron (in right) and a snapshot of the whole system (in bottom): for (a) $k_1 = 1.7$, $k_2 = 0.015$ from which synchronization is identified, (b) $k_1 = 0.7$, $k_2 = 0.18$ representing desynchronized state, (c) $k_1 = 0.5$, $k_2 = 0.015$ depicting chimera-like state. Here p_i bears the same connotation as x_i in Eq. (14). Figure reproduced with permission from [29].

$$\dot{x}_{i} = y_{i} + ax_{i}^{2} - x_{i}^{3} - z_{i} + J + k_{1} \sum_{j=1}^{N} A_{ij}(x_{j} - x_{i}) + k_{2}(v_{s} - x_{i}) \sum_{j=1}^{N} B_{ij}\Gamma(x_{j}),
\dot{y}_{i} = 1 - dx_{i}^{2} - y_{i},
\dot{z}_{i} = c(b(x_{i} - x_{0}) - z_{i}), \quad i = 1, 2, \dots N.$$
(14)

Here a=3.0, d=5.0, c=0.005, b=4.0, $x_0=-1.6$ and J=3.25 are chosen so as to keep the neurons in multi-scale chaotic dynamics and $v_s=2.0$ is taken so that the chemical coupling remains excitatory. Besides, A_{ij} and B_{ij} are the adjacency matrices respectively associated to the neuronal connections based on electrical and chemical synapses within and across the communities and k_1 , k_2 are the corresponding coupling strengths. Fig. 7 shows how dynamical behavior of the whole network varies for changes in the values of k_1 and k_2 . For instance, whenever $k_1=1.7$ and $k_2=0.015$, the network experiences coherent state which is shown in Fig. 7(a) while plotting the spatiotemporal evolution of the membrane potentials p_i (here p_i refers to x_i in Eq. (14)) together with their snapshot and the typical time series of a particular neuron p_{100} . On the other hand, the neurons in all the communities are desynchronized if $k_1=0.7$ and $k_2=0.18$ (cf. Fig. 7(b)). But interestingly, chimera-like coexistence of coherence and incoherence in the network emerged, shown in Fig. 7(c) when $k_1=0.5$, $k_2=0.015$ were chosen.

In the following, we would also like to mention that a number of neuronal developments are detected not only among coupled neurons in the same brain region, but also amidst uncoupled neuron groups in the same or different cortical areas. Besides, recent research corroborates that the multilayer structure of networks is the best formulation of so many natural and artificial systems [102–109]. So, the evidences of multilayer structure in neuronal system [110–113] directs the authors of ref. [33,35] to consider a multilayer network of Hindmarsh–Rose neuronal models (cf. Eq. (3)) composed of two layers, one of which is altogether uncoupled and the other one plays the role of a medium through which the neurons in the uncoupled layer communicate, and this layer is coupled in regular mode (locally, nonlocally or globally) through electrical synapses. Chemical synapses (in presence of delay) are presumed to interconnect the replica nodes of the two layers. Thus the dynamical equations representing the uncoupled layer reads as:

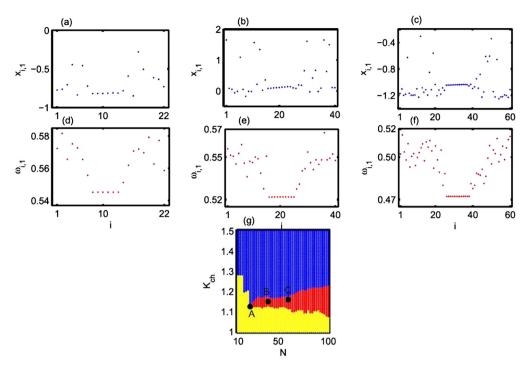


Fig. 8. Membrane potential $x_{i,1}$ snapshots representing chimera states in the uncoupled layer for (a) N=22, $K_{ch}=1.125$, (b) N=40, $K_{ch}=1.15$ and (c) N=60, $K_{ch}=1.16$; Lower panels (d,e,f) respectively depict the associated mean angular frequencies $\omega_{i,1}$ for N=22, 40, 60; (g) Two parameter phase diagram in the $K_{ch}-N$ plane. The regions corresponding to incoherent, chimera and coherent states are in yellow, red and blue respectively. Strength of incoherence is used to distinguish these dynamical states. The points A, B and C conform to the values of K_{ch} and N used in (a,d), (b,e) and (c,f) respectively. Figure reproduced with permission from [33].

$$\dot{x}_{i,1} = ax_{i,1}^2 - x_{i,1}^3 - y_{i,1} - z_{i,1} + K_{ch}(v_s - x_{i,1})\Gamma(x_{i,2}(t - \tau)),
\dot{y}_{i,1} = (a + \alpha)x_{i,1}^2 - y_{i,1},
\dot{z}_{i,1} = c(bx_{i,1} - z_{i,1} + e), \quad i = 1, 2, \dots, N,$$
(15)

and that for the coupled layer becomes

$$\dot{x}_{i,2} = ax_{i,2}^2 - x_{i,2}^3 - y_{i,2} - z_{i,2} + K_{ch}(v_s - x_{i,2})\Gamma(x_{i,1}(t - \tau)) + K_{el} \sum_{j=i-P}^{i+P} (x_{j,2} - x_{i,2}),
\dot{y}_{i,2} = (a + \alpha)x_{i,2}^2 - y_{i,2},
\dot{z}_{i,2} = c(bx_{i,2} - z_{i,2} + e), \quad i = 1, 2, \dots, N,$$
(16)

where $(x_{i,1}, y_{i,1}, z_{i,1})$ and $(x_{i,2}, y_{i,2}, z_{i,2})$ are the state variables for the neurons in uncoupled and coupled layers respectively, N being the number of neurons in each of the layers of network. K_{el} and K_{ch} respectively accounts for the electrical and chemical synaptic coupling strengths with τ being the time-delay due to the reaction times at chemical synapses. Here P is the coupling range and $R = \frac{P}{N}$ is entitled as coupling radius as before.

We will start while concentrating on the multilayer network comprising of uncoupled and globally coupled layers, that is when the coupling range $P = \frac{N}{2}$ is maximum in the coupled layer and there is no time delay in the chemical synapses.

In absence of the chemical synapses across the layers, the coupled layer easily becomes synchronized because of the global (all-to-all) interaction among the neurons with electrical synapses. Then the investigation on such a framework reveals that chimera state may emerge as a link between disordered and coherent states, in the uncoupled layer depending on the strength of the inter layer chemical synapses. Particularly, with an increment in the number of neurons in the uncoupled layer (and that in the coupled layer with replicas connected), an emergence of chimera states can be realized in the uncoupled layer. In order to explore this scenario, we start with minimal possible number of neurons in both the layers but chimera states could not be found for any value of K_{ch} unless $N \ge 22$, depicted in Fig. 8.

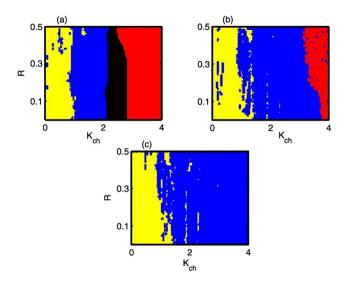


Fig. 9. Two parameter phase diagram in the $R - K_{ch}$ plane where incoherent, synchronous chimera, synchronous cluster, and coherent regions are respectively in yellow, blue, black, and red colors for (a) $\tau = 0.5$, (b) $\tau = 2.4$ and (c) $\tau = 4.0$. Here $K_{el} = 0.005$ is fixed with N = 105. Figure reproduced with permission from [35].

This essentially means chimera patterns can be realized in such a network formalism with as few as N=22 neurons in each layer. Whenever N=22, chimera states are observed for a narrow range of $K_{ch} \in [1.12, 1.13]$, otherwise promoting incoherent or coherent states for lower and higher K_{ch} respectively. The appearance of chimera state in the layer of uncoupled neurons for N=22 is explained by plotting the snapshot of membrane potentials $x_{i,1}$ in Fig. 8(a) for $K_{ch}=1.125$ where the layer spontaneously splits into incoherent domains mediated by a coherent one, resembling the characteristic of a chimera state. Increasing the number of neurons in the layers, not only the chimeras continue to be subsistent, but also it broadens the range of K_{ch} for which chimera emerges. The former assertion is illustrated through the snapshots of $x_{i,1}$ for N=40 and N=60 with $K_{ch}=1.15$ and $K_{ch}=1.16$ respectively in Figs. 8(b) and 8(c). For further confirmation of chimera patterns, mean angular frequency $\omega_{i,1}$ of the i-th neuron in the uncoupled layer is calculated as

$$\omega_{i,1} = \langle \dot{\phi}_{i,1} \rangle_t = \frac{x_{i,1} \dot{y}_{i,1} - y_{i,1} \dot{x}_{i,1}}{x_{i,1}^2 + y_{i,1}^2},$$

where $\phi_{i,1} = \arctan(y_{i,1}/x_{i,1})$ is the geometric phase of the *i*-th neuron, as discussed above and $\langle ... \rangle_t$ represents long time average. Figs. 8(d, e, f) respectively depict the mean angular frequencies $\omega_{i,1}$ (calculated over 5×10^5 time units after an initial transient of 3×10^5 units) of all the neurons corresponding to Figs. 8(a, b, c) that possess random values in the incoherent domains while exhibiting identical values for the coherent domain. In order to elucidate the latter scenario of nodal effect on K_{ch} , we plot the two-parameter phase diagram in the $N - K_{ch}$ plane in Fig. 8(g) for the range of $N \in [10, 100]$ and $K_{ch} \in [1.0, 1.5]$. From the figure, the expansion of the chimera region in terms of K_{ch} for increasing density N of neurons is obvious.

Without restraining the coupled layer to the fully coherent state under globally coupled formulation, the authors of ref. [35] detected two interesting dynamical states, namely synchronous chimera and synchronous cluster states between the layers. In these states, groups of neurons in each layer go through the same dynamical behavior with the same group of replica neurons in the other layer, while the individual layers exhibit chimera and cluster (synchronized) states respectively. Additionally, the influence of inter-layer chemical synaptic delay in eradicating the cluster, coherent patterns and reinstating the chimeras has also been explained. For instance, phase diagrams in the $R - K_{ch}$ parameter plane for different values of the time-delay τ are depicted in Fig. 9. Whenever the delay $\tau = 0.5$ is comparatively smaller, then according to Fig. 9(a), for all possible values of R, incoherent (in yellow), synchronous chimera (in blue), synchronous cluster (in black) and coherent states (in red) appear with increasing K_{ch} . Importantly enough, for a higher time-delay $\tau = 2.4$, cluster state does not exist in the parameter plane of Fig. 9(b) and the chimera state takes up that space in the phase diagram. As the delay τ further increases to $\tau = 4.0$, even the coherent state tends to

disappear from the figure (cf. Fig. 9(c)) and it is the chimera pattern that emanates as K_{ch} increases, irrespective of the value of the coupling radius R. This way the imminent time delay due to chemical synapses favors the appearance of synchronous chimera states while slackening the advancements of cluster or coherent states.

7. Summary and future prospects

Over the last two decades, complex biological networks [114] has been a rapidly growing research field because of its potential applications. The theory of complex biological network helps a lot to understand several emergent behavior arising in biological systems ranging from food webs to human brain. Through this review, we have tried to provide a profound excerpt of recent research efforts that explore the emergence of chimera states in networks of neuronal systems. We present our study with an everlasting intention of grasping how this phenomenal spatiotemporal pattern may emanate in neuronal networks depending on the variability in the fashion of interactions among the neurons. The applicabilities of chimera-like coexistence of coherence and incoherence from the viewpoint of neuronal activities are dealt with in Section 2. For example, chimera patterns have strong reflection to the neuronal bump states that correspond to localized regions of oscillatory coherence surrounded by incoherence. The natural phenomenon of unihemispheric slow wave sleep observed in some mammals and migratory birds has also got resemblance to the chimeric behavior. Moreover, various types of pathological brain states, such as Alzheimer's disease, epilepsy, autism, schizophrenia and brain tumors are reminiscent to dynamical chimera states found in networks of coupled oscillators.

In Section 3, we have described the FitzHugh–Nagumo and Hindmarsh–Rose neuronal models that are predominantly used in the nonlinear dynamics literature in order to explore collective dynamics that may arise in neuronal networks, in particular for the case of chimera-like patterns. A view of possible synaptic communication modes is provided in Section 4. Section 5 deals with the general model description of a neuronal network followed by the details of the quantitative measures (such as strength of incoherence, discontinuity measure, mean phase velocity and local order parameter) used to discriminate diverse dynamical phenomenon observed in the literature.

In Section 6, we have reviewed some recent studies investigating the origination of chimera-like states in neuronal systems, especially pinpointed on different synaptic interactional constructions of the networks. Section 6.1 deals with the emergence of chimera in neuronal networks in the sole presence of electrical synapses for which non-delayed, delayed and noisy electrical synapses are ascertained. The mechanisms of chimera transitions for only the chemical synapses are explained in Section 6.2 where the effects of time-delay due to the reaction times at chemical synapses as well as that of asymmetric excitatory synapses are investigated. Next Section 6.3 is devoted to the case in which chimera appears due to the presence of both electrical and chemical synapses. For this, the modular network structure based on the connectome of C. elegans is first considered followed by the multilayer formalism of neuronal networks comprising of coupled and uncoupled layers with and without chemical synaptic delays.

Because of its immense relevance in view of neuroscience, study of chimera states has got special attention of researchers over the years. Notably, since the seminal work by Kuramoto et al. [8] for ensemble of phase oscillators in the year of 2002, many of the crucial developments have been made, particularly in networks of neuronal systems. In spite of that, we would like to mention some of the significant routes of further research on chimera study in neuronal systems. For example,

- 1. Very recently, non-synaptic (ephaptic) communication among the neurons and emergence of alternating chimeras [115] has been shown to be fascinating enough to investigate. This is mainly because, so far, the inspection of such a peculiar pattern in neuronal networks has been mostly confined to the sole presence of synaptic interactions (electrical and/or chemical). Consequently, the possibility in manifestation of much more complex chimeric patterns owing to the simultaneity of synaptic and ephaptic interactions in neuronal networks, can be visualized as a promising future direction.
- 2. The study of control of chimeras in neuronal networks under chemical synaptic scenarios and independent of the network topology will be quite significant. Earlier, the authors of [116] described pinning control of coherent and incoherent domains in chimera patterns for ensembles of nonlocally coupled FitzHugh–Nagumo systems. Also a control strategy was presented [117] in nonlocally coupled FitzHugh–Nagumo elements, based on the inclusion of excitable dynamical units. Bick et al. [118] came up with a scheme based upon gradient dynamics that assisted the chimera patterns in attaining any desired positions, for coupled phase oscillators.

- 3. Next, the question of some theoretical foundations of chimera study under the non-linear chemical synaptic function as the interacting medium, is yet to be answered.
- 4. Also the issue of robustness of chimera states in neuronal systems against structural perturbations in presence of chemical and/or both electrical and chemical synapses is still unresolved.
- 5. The neuronal interaction mechanism through synapses are not really static. Rather, the connectivity patterns are sporadic that changes over time. But, because of its complexity, so far almost all the works on chimera states in neuronal systems have neglected this issue of time varying inter-connections among neurons and presumed static persistent network topologies only. So, it would be really significant to investigate the possible emergence of chimera-like patterns in neuronal networks that contemplates with temporal synaptic connections.
- 6. Few experimental verifications of chimera states have been done while considering setups as networks of optoelectronic oscillators, mechanical oscillators (metronomes), electronic circuits etc. But from the neurobiological point of view, there is no experimental verification on chimera states done yet. So, experimental detection of chimera states may lead to more interesting prospects in neuroscience.
- 7. Although there exists a few works concerning basin of attraction for the chimera states [119,120], precise study on the influence of initial conditions in inducing chimera patterns in neuronal networks is missing.
- 8. Because of the severe complexity of brain network, chimera studies should also aim to explore the same in more complex topologies, particularly, in networks of interconnected networks of neuronal systems.
- 9. Slow-fast dynamics are often present in neuronal systems. It will be very interesting to study whether multi time scale separation is a prerequisite criteria for the emergence of chimera states in such ensembles. Also in this regard, one can investigate different types of chimera patterns for varying bursting and spiking regimes.

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