

Flexible patterns of information transfer in frustrated networks of phase oscillators

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Abstract Brain networks are characterized by flexible patterns of pairwise correlations and information exchange between different brain regions. Such dynamic patterns are crucial for an efficient response of the brain to environmental and cognitive demands. We here propose that the collective oscillations in the brain can provide a mechanism to control dynamical interactions and the exchange of information across brain networks. In particular, we show that the phase difference between oscillatory activities in different brain regions determines the transmission of neural signals. To further corroborate this, we study a network of coupled oscillators with repulsive couplings and show that the amount of information transfer between the nodes is determined

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by the phase differences among them. The emergence of multiple (locally) stable states due to the frustration makes it possible to change the patterns of information transfer between the nodes by means of the switching between different stable states. Our results indicate that frustration can be the mechanism through which large scale brain networks control the effective connectivity and the routes for the information transfer between different brain regions.

Keywords Information transfer · Frustration · Functional networks

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1 Introduction

A prominent feature of the brain networks is that despite to the fixed structure, the effective dynamical interactions between the nodes and the routes for information transfer are subject of a continual change over time [1–3]. This variability in the functional connectivity is crucial for the brain networks to efficiently employ the local networks in multiplex tasks and adaptively respond to the continual changes in the environment. It is hypothesized that the phase relation between oscillatory activities of local brain networks could determine the mutual influence and provide a means for the control of the information transfer between brain regions [4–6]. Brain oscillations are observed in the brain circuits at different spatial and temporal scales [7, 8]. The collective oscillations divide the time into the alternating windows of low and high excitability and entail different response to the stimuli impacting at different phases of oscillations. Phase relation between oscillatory activities of the two connected regions then could determine the response of the network to the signal coming from the other network and could quantify the efficacy of the directed functional link between the two regions [5, 9–13]. Despite the abundance of experimental and theoretical evidences in support of the role of phase relation in the effective connectivity, it is not well-known through which mechanism the phase relation itself can be dynamically changed and controlled [5, 14]. Networks of coupled oscillators have been extensively used to model a wide variety of biological, social and physical networks and have successfully described the different dynamical collective behavior seen in the realistic networks [15–20]. In a simple framework, if the couplings between pair of oscillators are attractive, the oscillators tend to evolve in-phase. This sort of connections are able to synchronize a population of inter-connected oscillators if the couplings are enough strong to overcome possible disparity in the natural frequency of the oscillators [21–23]. On the other hand, repulsive couplings drive any pair of the oscillators to anti-phase state [24–28]. In this case larger networks show a nontrivial behavior due to the inconsistent competing effects of different connections that lead to the emergence of a frustrated state with multitude of locally stable dynamical states in the system [29–33].

Frustration exists as a ubiquitous phenomenon in the nature, and is has been observed in different fields of scientific literature, such as physical [4, 34–

44] and biological and biological networks [32, 45]. Although frustration arises in many physical systems, but it is most studied in the context of interacting magnetic systems, where the geometry of the lattice and/or the nature of the interactions make the simultaneous minimization of each term contributing to the energy impossible [46]. Frustration has been introduced as the consequence of conflicting interactions that make the energy of the ground states higher than that of unfrustrated system. Therefore, a system is said to be frustrated whenever it cannot minimize its total energy by minimizing the energy of each pair of interacting degrees of freedom. Moreover, frustration also enforces a large multiplicity of local minima in energy landscape, often associated with an excess entropy at zero temperature. So forth it increases dynamical repertoire of the networks [30] and plays an important role in the stabilization of critical phases [47], metastability [31, 32], and multi-stability [33].

In this paper, we questioned if the presence of multiple locally stable states in the frustrated networks with small number of degrees of freedom (nodes) can lead to a flexible pattern of information transfer. To this end we studied small networks of phase oscillators with repulsive couplings and showed that different phase differences between the nodes in these networks, lead to different effective connectivity–pattern of information exchange between the oscillators. Repulsive coupling between the nodes is realized by considering a delay in the transmission of the signals between any pair of the oscillators. In a suitable range of delays the antiphase state can be stabilized for the isolated pair that leads to frustration when the motif consisted of more than two oscillators. We inspected how the information transfer in these networks depends on the phase difference between the oscillators. Frustration have been observed in the recent experiments on the functional connectivity of large scale brain networks [48, 49] and this study highlights a possible relation between the frustrated dynamics and the dynamical effective connectivity and the flexible pattern of information routing in brain circuits.

2 Methods

2.1 Dynamical model

We considered a network consisting of N pulse-coupled "Winfree oscillators" [50, 51] with phase variables $\{\theta_i\}_{i=1,\dots,N}$, $0 \leq \theta_i < 2\pi$ and the dynamics governed by

$$\dot{\theta}_i = \omega_i + Q(\theta_i) \frac{\varepsilon}{N} \sum_{j=1}^N P(\theta_j) + \xi_i(t) \quad (1)$$

Here Over-dot shows the time derivative, ε is a constant parameter to control the coupling strength to noise ratio, and it is considered identical for all the connections. We also assumed that the natural frequencies of all the oscillators are identical $\omega_i = \omega$. The oscillators are pulse-coupled, i.e., each oscillator

emits a pulse whenever it passes 2π and the pulse arrives in the target oscillator after a time τ which is an important parameter in driving the system into a frustrated state [52]. This was realized in the model by considering $P(\theta(t)) = \delta(\theta(t - \tau))$, in which δ is the Dirac Delta function.

The phase response curve (PRC) function $Q(\theta)$ measures the degree of advance or delay of the phases when the oscillators are perturbed. In similar modeling researches, the PRC function $Q(\theta)$ is usually considered as

$$Q(\theta) = \sin(\beta) - \sin(\theta + \beta) \quad (2)$$

such that the PRC vanishes at $\theta = 0$, which is natural in neuronal modeling. The oscillator is called type-II for $\beta < \pi/2$ and $\beta = \pi/2$ is related to the case type-I oscillators [23, 53–58]. Without loss of generality, we have considered type-II oscillator with $\beta = 0$ in the rest of the manuscript. Finally, $\xi_i(t)$ is a Gaussian white noise with zero mean and unit variance. The equations for the governing dynamics of the oscillators can therefore be written as

$$\dot{\theta}_i(t) = \omega - \sin(\theta_i(t)) \frac{\varepsilon}{N} \sum_{j=1}^N \delta(\theta_j(t - \tau)) + \xi_i(t) \quad (3)$$

2.2 Information measurement

After the introduction of Transfer Entropy (TE) by Schreiber [59], it has been increasingly used as a powerful tool to detect the transfer of information between two joint processes in different dynamical system, such as brain electrophysiological data [60–63]. This measure is independent of how this information is encoded.

Consider the system described by Eq.(3), consists of N interacting dynamical oscillators and suppose that we are interested to investigate the information flow from source oscillator θ_i to the destination oscillator θ_j , collecting the remaining systems in the vector $\psi = \{\theta_k\}_{k \neq i,j}$. As it is evident from different simulations in this manuscript, phase difference and so all the θ 's are stationary processes. We develop our framework under the assumption of stationarity, which allows to perform estimations replacing ensemble averages with time averages. Accordingly, $\theta_i(t)$, $\theta_j(t)$ and $\psi(t)$ denote the stationary stochastic state of the system at the moment t . Moreover, we denote $\theta_i^-(t) = [\theta_i(t-1) \ \theta_i(t-2) \ \dots]$, $\theta_j^-(t) = [\theta_j(t-1) \ \theta_j(t-2) \ \dots]$ and $\psi^-(t) = [\psi(t-1) \ \psi(t-2) \ \dots]$ as the vector variables representing the whole past of the system by now. Then, the transfer entropy from θ_i to θ_j conditioned to ψ is defined as:

$$\text{TE}(t) = \sum_{\theta_i \rightarrow \theta_j | \psi} p(\theta_j(t), \theta_j^-(t), \theta_i^-(t), \psi^-(t)) \log \frac{p(\theta_j(t) | \theta_j^-(t), \theta_i^-(t), \psi^-(t))}{p(\theta_j(t), \theta_j^-(t), \psi^-(t))} \quad (4)$$

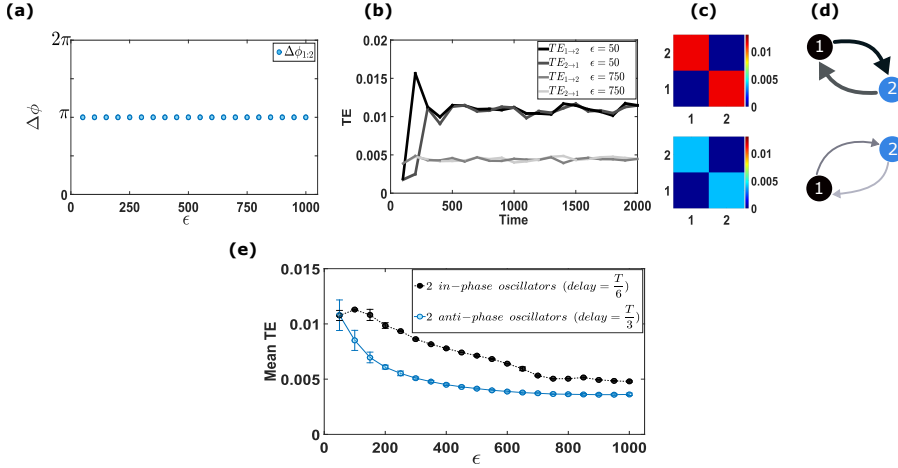


Fig. 1 Phase difference and transfer entropy for two reciprocally connected oscillators. (a) Mean phase difference between two oscillators as a function of ϵ , which remains equal to π for the range of coupling strength that we checked. (b) The time evolution of TE, for two different ϵ values. In (c) and (d) matrix and graph representation of average TE is shown for $\epsilon = 50$ and $\epsilon = 750$, respectively. Width of arrows in (d) indicate the strength of TE. In (e) average of TE for in-phase (black) and anti-phase (blue) states of two coupled oscillators as functions of ϵ . Anti- and in-phase states are achieved by setting $\beta = 2\pi/3$ and $\beta = \pi/3$, respectively

where the sum extends over all the phase space points forming the trajectory of the composite system. $p(\mathbf{a})$ is then the probability associated with the vector variable $\mathbf{a}$ while $p(b|\mathbf{a}) = p(\mathbf{a}, b)/p(\mathbf{a})$ is the probability of observing b knowing the values of $\mathbf{a}$. The conditional probabilities used in this equation can be interpreted as transition probabilities, quantifying to which extent the transition of the target system towards its present state is affected by the past states visited by the source system. Specifically, the TE quantifies the information provided by the past of the θ_i about the present of the θ_j that is not already provided by the past of θ_j or any other process included in ψ .

We used the MATLAB toolbox 'MuTE' [64] to calculate TE between the nodes with a method called 'BINNUE' among the other methods tested in [64], in the system of N oscillators whose evolution is governed by Eq.(1). This procedure employs binning technique to estimate entropy and non-uniform embedding to determine the most significant lag of variables. We approximated each vector $\theta_i^-(t)$ using the embedding vector $\theta_i^-(t) = [\theta_i(t-99) \ \theta_i(t-98) \ \dots \ \theta_i(t)]$ and calculated the information flow from the source element $\theta_i(t)$ to the destination system $\theta_j(t)$, [64].

3 Results

In all the systems considered here, the oscillators have similar natural frequency, and the connections are of similar coupling strength and time delay

in transmission of pulse to other oscillators. It was previously shown that for any identical pair of symmetrically coupled oscillators with delayed couplings, the stability of inphase or anti-phase state depends on the delay and slope of the coupling function [6, 27, 65, 66]. With the sinusoidal coupling used here, we chose time delay between $T/2$ and $3T/2$, where T is the period of the oscillations. This stabilizes anti-phase state for a system comprising of two mutually coupled oscillators and leads to frustration for the systems with more oscillators [29]. In the following we first study the information transfer for two coupled oscillators and then inspect the same property in the frustrated systems with more than two oscillators. We fix the delay and change the amplitude of the external noise and coupling strength and show how the phase difference between the oscillators affects communication between the oscillators.

3.1 Two coupled oscillators in anti-phase regime

We start our investigation by the study of two mutually connected oscillators. Figure 1(a) shows the mean phase difference between the two oscillators as a function of the coupling strength for different values of the noise amplitude. As expected, the mean phase difference is equal to π which indicates oscillators are in an anti-phase state. In this state just like the inphase state the system is dynamically symmetric, that is the system is invariant under the permutation $1 \leftrightarrow 2$. Therefore, it is expected that the information transfer is also symmetric and has no preferred direction. This is verified in Fig. 1(b) where we have shown time resolved transfer entropy (TE) for two exemplar values of coupling strength and noise amplitude. For more clarity and later convenience, we have shown the effective network or the effective connectivity matrix whose elements show the amount of information transfer between any pair of the network (Fig. 1)(c and d). It is seen that information transfer is symmetric in two directions and there is no preferred direction in the system. It is notable that the asymmetric information transfer between a pair of connected oscillators can be induced by breaking the symmetry using non-identical oscillators or with non-sinusoidal interaction function [12, 67].

Another observation in Fig. 1(b) is that higher ratio of coupling strength to noise amplitude leads to lower values of information transfer in two directions. This is notable that this result also holds for the case of attractive coupling when inphase state is stable. As we will later observe, this result is not dependent to the number of oscillators in the synchronized state with attractive connections and the same dependence of the information transfer to the noise and coupling strength can be observed in networks with larger oscillators. However, for the networks with desynchronizing connections the dependence of the information transfer on the ratio of the coupling constant to noise amplitude is not trivial and depends on the number of oscillators and the phase lag between the nodes.

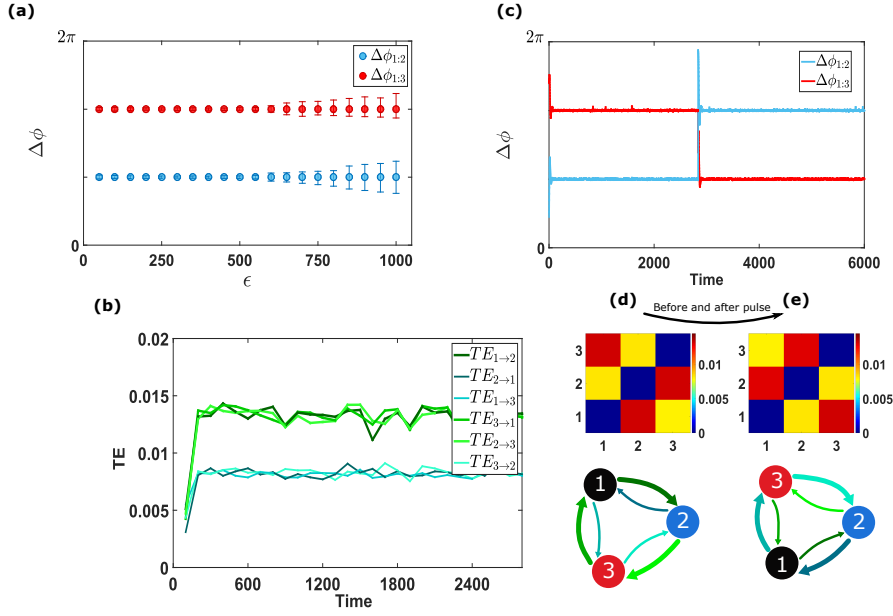


Fig. 2 Phase difference and Transfer Entropy for three coupled oscillators. (a) Mean phase differences between pair of oscillators in a motif consisting of three oscillators. (b) TE values for a network of three oscillators, shows that TE between nodes is dependent on the phase differences $\Delta\phi = \frac{2\pi}{3}$ and $\Delta\phi = \frac{4\pi}{3}$. Here $\epsilon = 150$. (c) Evolution of phase differences in three-oscillator motif with $\epsilon = 150$. External perturbation at $t = 3000$ causes a change in phase differences. An arbitrary node has been chosen as a reference node, and relative phases are shown with respect to the reference node. In (d) and (e) mean TE values before (left) and after (right) the external pulse is represented. Lower graphs indicate average TE values before and after imposing the pulse. As mentioned in 1 the width of arrows display the amount of TE between nodes.

3.2 Three coupled oscillators

We then considered a fully connected motif composed of three oscillators with the set of parameters and time delay for which any pair of neurons favor antiphase locking. But this state is not achievable for three oscillators and instead, the phases lock in a state at which the phases are equally spaced with $\Delta\phi = -2\pi/3$ and $\Delta\phi = 2\pi/3$. Analytic investigation for such a system confirms stability of this *splay state* (see supplementary material of Ref. [29]). Note that with three oscillators this state has a two-fold degeneracy with different arrangement of phases 123 and 132, where phase difference between two successive oscillators is $2\pi/3$.

The pairwise phase difference versus coupling strength for one of stable states is shown in Fig. 2(a), for different values of coupling strength to noise amplitude ϵ . The main point for this system is that the pairwise permutation symmetry is violated here, and this asserts the possibility of asymmetry in the information transfer in two directions and the presence of preferred directions for information transfer between pair of nodes.

The results for time resolved TE between the oscillators in Fig. 2(b) confirms that the TE for two directions between pair of oscillators is not equal. Moreover, the directional TE for those pairs that have equal phase differences is similar, i.e., amount of information transfer can be uniquely determined by the phase difference. This means that switching between the two stable states (123 and 132) can change the effective connectivity and the preferred direction for information flow between and pair of oscillators. We tested this by applying a simultaneous pulse on two oscillators as is shown in Fig. 2(c). The pattern of phase difference was changed if the pulse was not applied on all the oscillators. The change in the phase difference between the oscillators, alters the information transfer between the oscillators. As is evident from Fig. 2(c) and effective connectivity matrix shown in Fig. 2(d-e) in the case of three-oscillator motif, this change in the phase differences reverses the preferred direction of the information flow and consequently converts the effective connectivity matrix.

We also checked that the main results stated above are valid for different values of coupling strength and noise amplitude. To this end we varied the ratio ϵ and calculated TE for the pair of oscillators with two different phase differences. As is shown in Fig. 5(a) the dependence of the TE to ϵ is not monotonic, but the asymmetry of the information transfer and the ability of the network to change effective connectivity remains valid for all values of ϵ that we checked.

3.3 networks with larger number of oscillators

The cases of two- and three-neuron motifs are examples for two prototypical properties that emerge in the networks with repulsive couplings. In these two motifs, information transfer between pair of coupled neurons can be either symmetric or asymmetric based on the phase difference between the oscillators. In the latter case, it is possible to change the effective connectivity and the preferred direction of information transfer with suitably applied external stimulation. In the following we test two other networks with greater number of oscillators to show that these results can predict the properties of effective connectivity in such networks. In Figs. 3 and 4 we have shown the results for 5 and 8 oscillators, respectively. Same as the three-oscillator network, the most stable state is that with phases equally spaced around the circle with $2\pi/N$ phase difference between the pairs. The information transfer between any pair of the nodes is dependent to their phase lag, and the pairs with similar phase lag have the same amount of information transfer. Since the number of the degenerate states in the fully connected network of the oscillators is $(N - 1)!$ there are $4!$ and $7!$ different states for $N = 5$ and $N = 8$, respectively. Note that these are only the number of degenerate splay states with equally spaced phases and don't consider other locally stable states with supposedly smaller basin of attraction [33]. With external pulses, it is possible to switch between these states as is shown in Fig. 3. In each state the matrix of effective connectivity and preferred direction of information transfer between the nodes

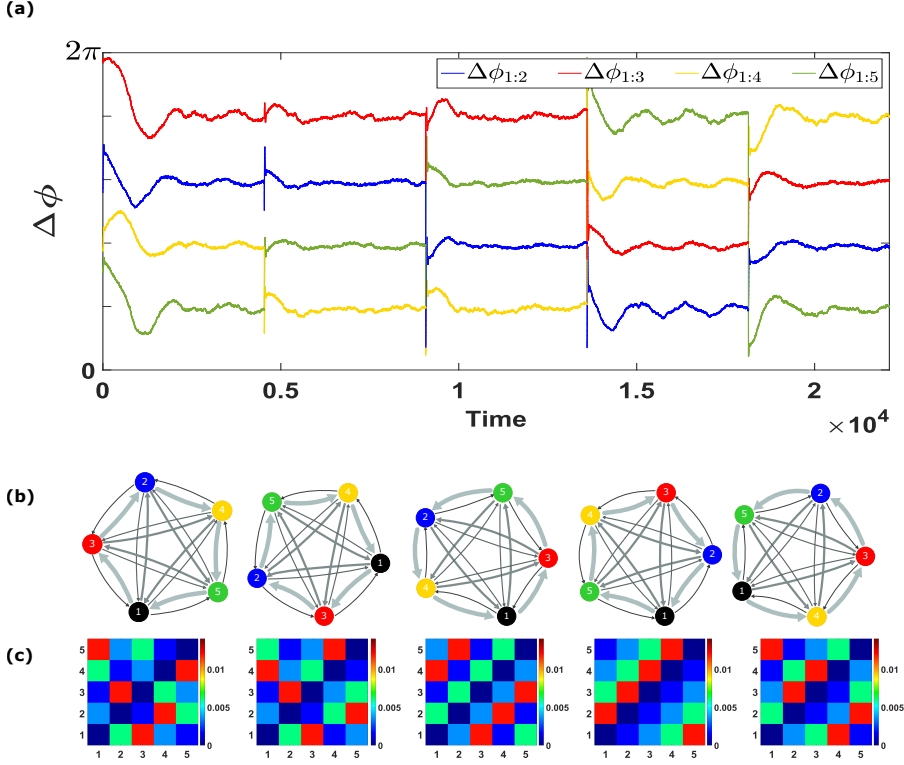


Fig. 3 Phase difference and TE values in a network of five identical oscillators. (a) The stable state of this system before and after external arbitrary perturbations exerted at different times. Five locally stable states are realized by external pulses with phase difference $\frac{2\pi}{5}$ between pair of nodes. Average TE is represented in (b) and (c) for the states that are realized in (a). We have set $\epsilon = 150$.

is different. Note that only a fraction of all accessible states are realized in our simulations but in principle with suitable pattern of external stimuli all of them are in principle achievable.

To get more insight into the dynamics of the frustrated networks and to highlight its difference with the synchronized state, we have shown the dependence of the information transfer on the ratio of the coupling strength to noise amplitude ϵ in Fig. 5 for the synchronized and frustrated networks. In the synchronized state there is only a single globally stable state and for all the pairs the phase lag is zero (with a small deviation due to the noise). In this case the information transfer between all the pairs is equal regardless of the direction, and it decays with increasing ϵ just like two-oscillator motif. For the frustrated state, however, TE shows a non-trivial dependence on the ϵ that differs for the pairs with different phase lags and also changes with the number of the oscillators in the networks as is seen in Fig. 5(b).

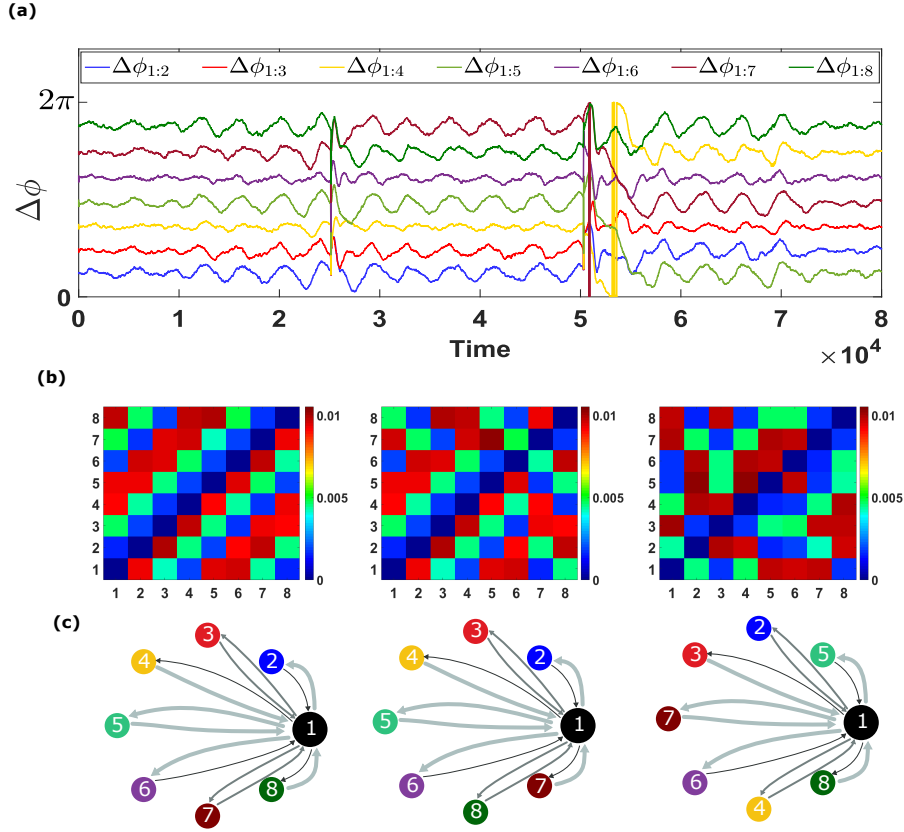


Fig. 4 Locally stable states and TE values in a network of 8 oscillators. (a) Phase differences between nodes before and after 2 random external pulses. Each pair of oscillators take $\Delta\phi \simeq \frac{2\pi}{8}$ in this state. Here $\epsilon = 250$. (b) Average TE between nodes for the states realized in (a). Under these conditions, 3 different values for TE can be observed. (c) Graphs which represent average TE values between one arbitrary node and all other nodes in the network. As in part (a), here node 1 is chosen to be the reference node and TE between these oscillators and the others are represented by the links. Width of each arrow corresponds to a TE value. Here we put $\epsilon = 250$.

4 Discussion

One of the intriguing features of brain dynamics is that its collective dynamics continuously changes despite the fact that the brain structure is effectively fixed at least in the short time scales over which the dynamics changes. This variability can be observed both in dynamics of the local neuronal ensembles and in the large-scale brain networks. In the local scale, neuronal oscillations show a high degree of variability and local oscillations wax and wane in an intermittent manner with a highly variable amplitude and the frequency [68,69]. In the large-scale brain networks, functional connectivity which quantifies the inter-regional coherence and the communication between brain areas is not

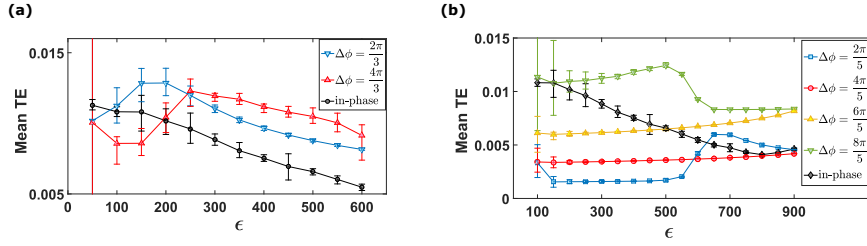


Fig. 5 Mean TE values as function of ϵ for 2 motifs with 3 and 5 nodes, in both inphase and out-of-phase (frustrated) regime. (a) In the case of 3 identical oscillators, mean TE values are shown for $\Delta\phi = \frac{2\pi}{3}$ in blue and red for $\Delta\phi = \frac{4\pi}{3}$. For the in-phase state all the connections have zero phase difference and the TE for all the links are the same. This value of TE for the inphase state is shown in black. (b) Same as (a) for 5 coupled oscillators, colored curves display TE values for frustrated regime, and the black one is for synchronous state. It is seen that TE value of in-phase oscillations decreases with ϵ while its dependence is not monotonic for frustrated state.

static and changes over time. However, there are a handful of distinct functional connectivity patterns that are specific for the state of the brain and are consistent across time and subjects [70]. It is recently shown that even in resting state, brain's functional connectivity changes and switches between several specific patterns [71]. It is not still known which network and neuronal properties determines these functional connectivity patterns and how the brain controls the switching between these quasi-stable patterns. Several models and mechanisms have been proposed to explain the flexible pattern of coherence and time-dependent collective dynamics of the brain [72–76]. In this manuscript we presented a minimal model composed of a few coupled oscillators that is capable to produce several locally stable phase locking patterns and can switch between the different states by the external perturbations. Our model is based on the fact the repulsive pairwise connections between the nodes of oscillators network leads to co-existence of several locally stable states through a mechanism known as dynamical frustration. We hypothesized that the rich dynamics of the frustrated network of the coupled oscillators and coexistence of the several meta-stable states can underlie the prominent feature of the brain networks that switch between different functional connectivity patterns based on the cognitive demand or spontaneously. We showed that in our model the amount of information transfer between the nodes can be uniquely determined by the phase relations between the nodes. Moreover, the information transfer between the nodes is not symmetric while the phase difference between the pair of the nodes excludes permutation symmetry. Therefore, at each state, the preferred direction for information transfer determines the sources and the targets of the information transfer. We also showed that the by perturbing the system, it is possible to switch between the different states and accordingly change the pattern of information exchange in the network.

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Conflict of interest

The authors declare that they have no conflict of interest.

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5 Statements and Declarations

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5.2 Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

5.3 Author Contributions

Saideh Khatami conducted the simulations and analyzed data, Ehsan Bolhasani conceived the study, analyzed data and wrote the first draft of the manuscript, Matjaž Perc conceived the study and wrote the manuscript, Alireza Valizadeh conceived the study, analyzed data, and wrote the manuscript.

5.4 Data Availability

The datasets generated during and/or analyzed during the current study are not publicly available at this stage, but are available from the corresponding author on reasonable request.