



Flexible patterns of information transfer in frustrated networks of phase oscillators

Saideh Khatami · Ehsan Bolhasani ·
Matjaž Perc · Alireza Valizadeh

Received: 3 August 2022 / Accepted: 24 September 2022 / Published online: 6 October 2022
© The Author(s), under exclusive licence to Springer Nature B.V. 2022

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 dif-

ference 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 by the phase differences. 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.

S.Khatami · A. Valizadeh
Department of Physics, Institute for Advanced Studies in
Basic Sciences (IASBS), Zanjan, Iran

E. Bolhasani
Department of Physics, University of Isfahan, Isfahan
81746-73441, Iran

M. Perc
Faculty of Natural Sciences and Mathematics, University
of Maribor, Koroška cesta 160, 2000 Maribor, Slovenia

M. Perc
Department of Medical Research, China Medical
University Hospital, China Medical University, Taichung
404332, Taiwan

M. Perc
Alma Mater Europaea, Slovenska ulica 17, 2000 Maribor,
Slovenia

M. Perc
Complexity Science Hub Vienna, Josefstädterstraße 39,
1080 Vienna, Austria

A. Valizadeh (✉)
Pasargad Institute for Advanced Innovative Solutions
(PIAIS), Tehran 1991633357, Iran
e-mail: valizade@iasbs.ac.ir

Keywords Information transfer · Frustration ·
Functional networks

1 Introduction

A prominent feature of the brain networks is that despite 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 can determine the response of the network to the signal coming from the other network and quantifies 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 [15–23]. 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 interconnected oscillators if the couplings are enough strong to overcome possible disparity in the natural frequency of the oscillators [24–26]. On the other hand, repulsive couplings drive any pair of the oscillators to anti-phase state [27–31]. In this case, larger networks show a non-trivial 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 [32–36].

Frustration exists as a ubiquitous phenomenon in the nature, and it has been observed in different fields of scientific literature, such as physical [4, 37–47] and biological networks [35, 48]. Although frustration arises in many physical systems, it is most studied in the context of interacting magnetic systems, where the geometry of the lattice and/or the nature of the interactions makes the simultaneous minimization of each term contributing to the energy impossible [49]. 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 [33] and plays an important role in the stabilization of critical phases [50], metastability [34, 35], and multi-stability [36].

In this paper, we questioned if the presence of multiple locally stable states in the frustrated networks with small number of degrees of freedom 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 anti-phase 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 [51, 52], 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” [53, 54] 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 [55]. 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 phase when the oscillator is perturbed by a brief stimulation at phase θ . In general, the PRC function $Q(\theta)$ can be considered as

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

such that the PRC vanishes at $\theta = 0$, which is a realistic assumption in neuronal modeling. The oscillator is type-II for $\beta < \pi/2$ and $\beta = \pi/2$ is related to the case type-I oscillators [25, 26, 56–60]. Type-I oscillators have a strictly positive PRC meaning that the external perturbations advance the phase regardless of the phase at which they are imposed. For type-II oscillators, perturbation may advance and delay the phase and hence PRC can take both positive and negative values. Without loss of generality, we have considered type-II oscillators 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 [61], 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 [62–65]. 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:

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

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 toward 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' [66] to calculate TE between the nodes with a method called 'BINNUE' among the other methods tested in [66], 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 target system $\theta_j(t)$, [66].

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 in-phase or anti-phase state depends on the delay

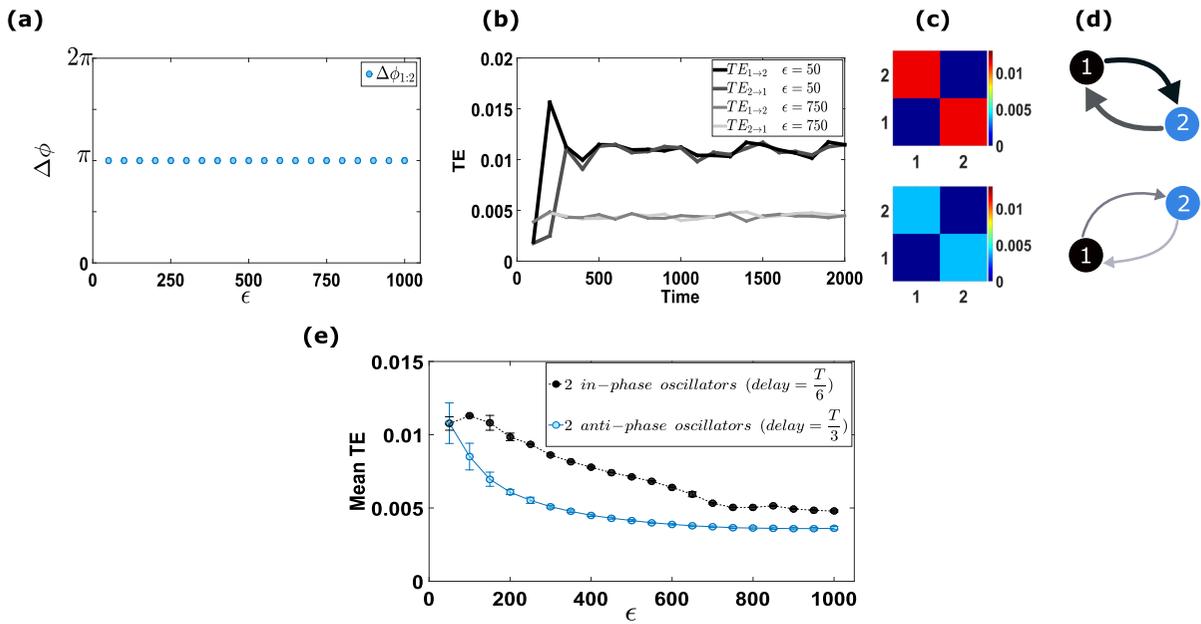


Fig. 1 Phase difference and transfer entropy for two reciprocally connected oscillators. **a** Mean phase difference between two oscillators as a function of ϵ , which remains equal to π for the range of coupling strength that we checked. **b** The time evolution of TE, for two different ϵ values. In **c** and **d**, matrix and graph representation of average TE is shown for $\epsilon = 50$

and $\epsilon = 750$, respectively. Width of arrows in **d** indicates 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 $\tau = T/3$ and $\tau = T/6$, respectively

and slope of the coupling function [6,30,67,68]. 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 two mutually coupled oscillators and leads to frustration for the systems with more oscillators [32]. 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 1a 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 in-phase 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. 1b 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, d). It is seen that information transfer is symmetric in two directions and there is no preferred direction for information flow 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 [12,69].

Another observation in Fig. 1b is that higher ratio of coupling strength to noise amplitude leads to lower

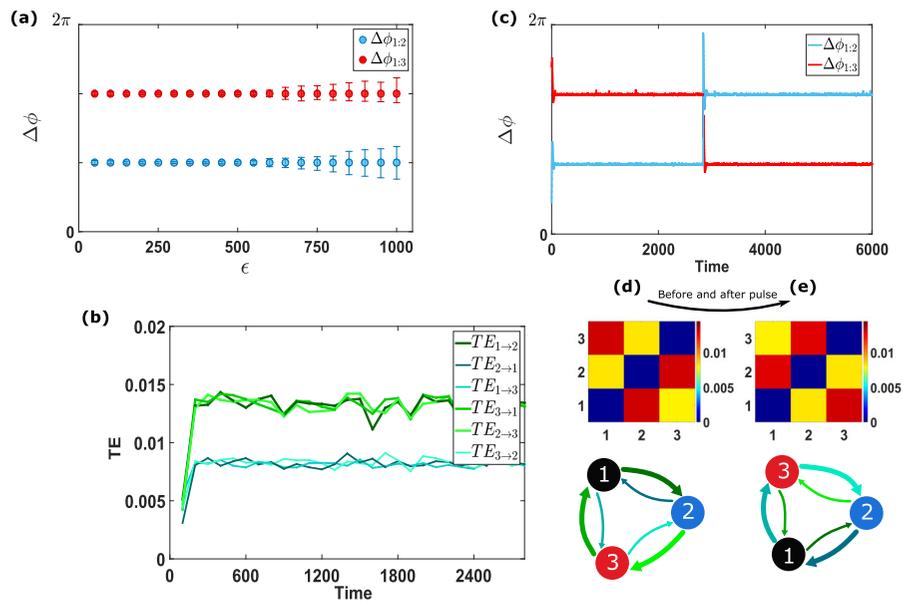


Fig. 2 Phase difference and transfer entropy for three coupled oscillators. **a** Mean phase differences between pair of oscillators in a motif consisting of three oscillators. **b** TE values for a network of three oscillators, showing that TE between nodes is dependent on the phase differences $\Delta\phi = \frac{2\pi}{3}$ 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 are 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

values of information transfer in two directions. This is notable that this result also holds for the case of attractive coupling when in-phase state is stable. As we will later observe, this result is not dependent on 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.

3.2 Three coupled oscillators

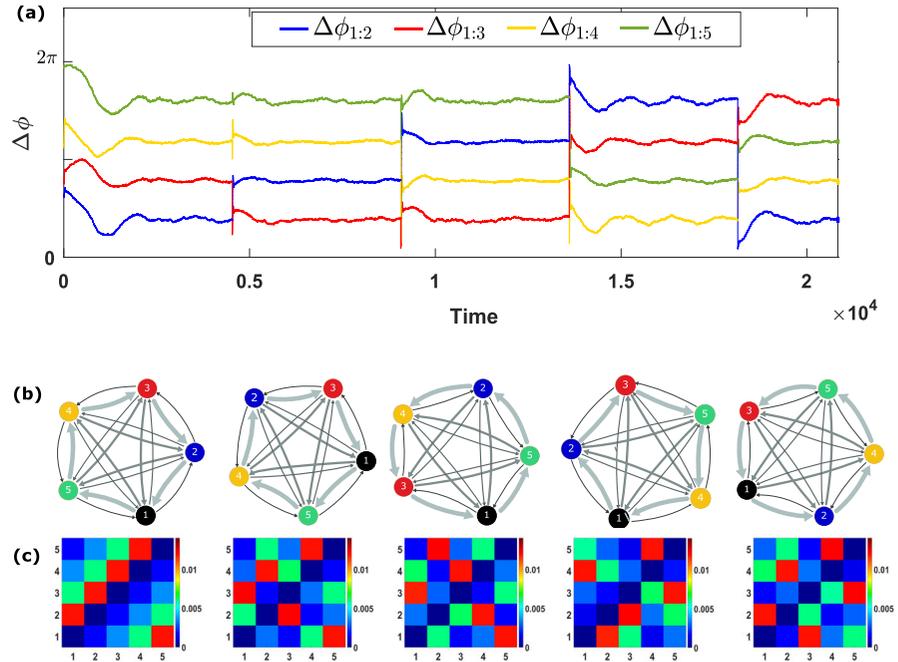
We then considered a fully connected motif composed of three oscillators with the set of parameters and time delay for which any pair of neurons favor anti-phase locking. But this state is not achievable for three oscillators and instead, the phases lock in a state at which

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. [32]). Note that with three oscillators this state has a twofold 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. 2a, 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. 2b confirm 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

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 $\epsilon = 150$



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. 2c. The pattern of phase difference 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. 2c and effective connectivity matrix shown in Fig. 2d, 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 whether 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. 5a, 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 remain 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. We ordered the oscillators based on their phase difference with an arbitrary node, node 1, before an external pulse is applied. It is seen that 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 [36]. With

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 all the nodes and **d** between one arbitrary node and all other nodes in the network

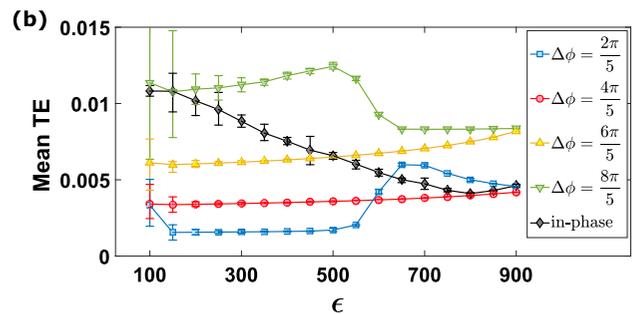
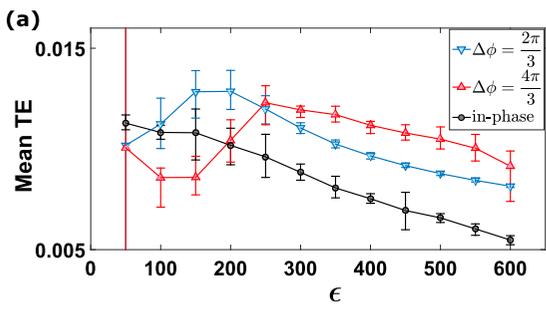
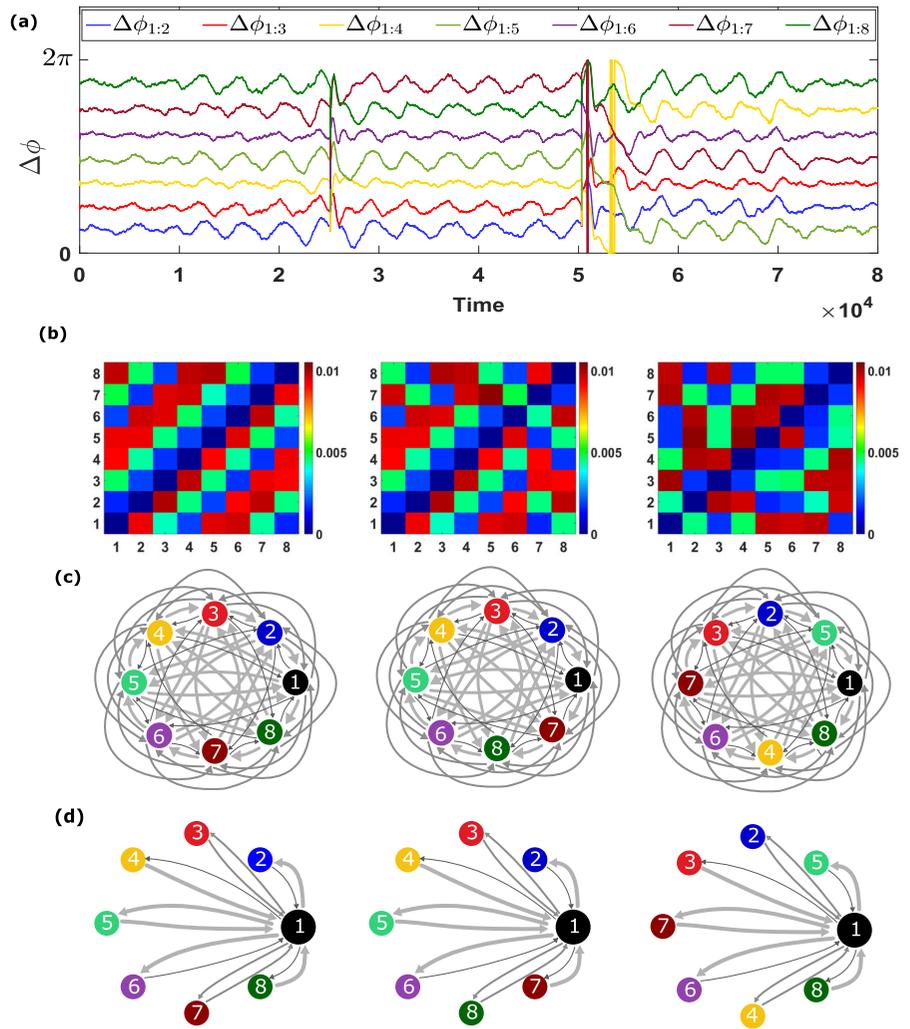


Fig. 5 Mean TE values as function of ϵ for 2 motifs with 3 and 5 nodes, in both in-phase and out-of-phase (frustrated) regime. **a** In the case of 3 identical oscillators, mean TE values are shown for $\Delta\phi = \frac{2\pi}{3}$ in blue and red for $\Delta\phi = \frac{4\pi}{3}$. For the in-phase state, all the connections have zero phase difference and the TE for all the links are the same. This value of TE for the in-phase

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

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 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. 5b.

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 the oscillations wax and wane in an intermittent manner with a highly variable amplitude and the frequency [70, 71]. In the large-scale brain networks, functional connectivity which quantifies the inter-regional coherence and the communication between brain areas is not 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 [72]. It is recently shown that even in resting state, brain's functional connectivity changes and switches between several specific patterns [73]. It is not still known which network and neuronal properties determine these functional connectivity pat-

terns 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 [74–78]. In this manuscript, we presented a minimal model composed of a few coupled oscillators that is capable of producing 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 coexistence 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 to switch between different functional connectivity patterns based on the cognitive demand or spontaneously.

In the physical frustrated systems like spin systems, the minimization of the energy of interaction between pair of nodes increases energy of the other links and the competence between the different links for minimizing the energy leads to the multitudes of meta-stable states in the energy landscape [79]. In the network of coupled oscillators, a similar energy-like function can be defined that is widely used to determine stability of the synchronized states in the networks of coupled oscillators [80]. The same concept, minimization of an energy-like function, is proposed as a hypothetical fundamental principle that optimizes the organization of the nervous system for the coding and the process of the information received from the environment [81, 82]. It is worth noting that concept of energy in the dynamical biological systems might be different from the physical energy and it is just a scalar function, minima of which show the stable states of system.

Our results show that in 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 violates the permutation symmetry. Therefore, at each state, the preferred direction for information transfer determines the sources and the targets of the information transfer. Our simple model reproduced a prominent property of the biological neural networks, that is, the ability to switch between different dynamical states and different func-

tional connectivity patterns based on the cognitive and environmental demands. We showed that by perturbing a frustrated network, it is possible to switch between the states with different phase-difference relations between the nodes and accordingly change the pattern of information exchange in the network.

Author contributions SK conducted the simulations and analyzed data, EB conceived the study, analyzed data, and wrote the first draft of the manuscript, MP conceived the study and wrote the manuscript, AV conceived the study, analyzed data, and wrote the manuscript.

Funding M.P. was supported by the Slovenian Research Agency (Grant Nos. P1-0403 and J1-2457).

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.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

References

- Edelman, G.M., Gally, J.A.: Degeneracy and complexity in biological systems. *Proc. Natl. Acad. Sci.* **98**(24), 13763–13768 (2001). <https://doi.org/10.1073/pnas.231499798>
- Battaglia, D., Witt, A., Wolf, F., Geisel, T.: Dynamic effective connectivity of inter-areal brain circuits. *PLoS Comput. Biol.* **8**(3), 1–20 (2012). <https://doi.org/10.1371/journal.pcbi.1002438>
- Park, H.J., Friston, K.: Structural and functional brain networks: from connections to cognition. *Science* **342**(6158), 1238411 (2013). <https://doi.org/10.1126/science.1238411>
- Pauling, L.: The nature of the chemical bond-1992. *J. Chem. Educ.* **69**(7), 519 (1992). <https://doi.org/10.1021/ed069p519>
- Fries, P.: Rhythms for cognition: communication through coherence. *Neuron* **88**(1), 220–235 (2015). <https://doi.org/10.1016/j.neuron.2015.09.034>
- Pariz, A., Fischer, I., Valizadeh, A., Mirasso, C.: Transmission delays and frequency detuning can regulate information flow between brain regions. *PLoS Comput. Biol.* **17**(4), 1–24 (2021). <https://doi.org/10.1371/journal.pcbi.1008129>
- Buzsáki, G.: *Rhythms of the Brain*. Oxford University Press, New York (2006). <https://doi.org/10.1093/acprof:oso/9780195301069.001.0001>
- Buzsáki, G., Draguhn, A.: Neuronal oscillations in cortical networks. *Science* **304**(5679), 1926–1929 (2004). <https://doi.org/10.1126/science.1099745>
- Fries, P.: A mechanism for cognitive dynamics: neuronal communication through neuronal coherence. *Trends Cogn. Sci.* **9**(10), 474–480 (2005). <https://doi.org/10.1016/j.tics.2005.08.011>
- Hahn, G., Bujan, A.F., Frégnac, Y., Aertsen, A., Kumar, A.: Communication through resonance in spiking neuronal networks. *PLoS Comput. Biol.* **10**(8), 1–16 (2014). <https://doi.org/10.1371/journal.pcbi.1003811>
- Rezaei, H., Aertsen, A., Kumar, A., Valizadeh, A.: Facilitating the propagation of spiking activity in feedforward networks by including feedback. *PLoS Comput. Biol.* **16**(8), 1–27 (2020). <https://doi.org/10.1371/journal.pcbi.1008033>
- Pariz, A., Esfahani, Z.G., Parsi, S.S., Valizadeh, A., Canals, S., Mirasso, C.R.: High frequency neurons determine effective connectivity in neuronal networks. *Neuroimage* **166**, 349–359 (2018). <https://doi.org/10.1016/j.neuroimage.2017.11.014>
- Ziaemehr, A., Zarei, M., Valizadeh, A., Mirasso, C.R.: Frequency-dependent organization of the brain's functional network through delayed-interactions. *Neural Netw.* **132**, 155–165 (2020). <https://doi.org/10.1016/j.neunet.2020.08.003>
- Avena-Koenigsberger, A., Misic, B., Sporns, O.: Communication dynamics in complex brain networks. *Nat. Rev. Neurosci.* **19**(1), 17–33 (2018). <https://doi.org/10.1038/nrn.2017.149>
- Cabral, J., Hugues, E., Sporns, O., Deco, G.: Role of local network oscillations in resting-state functional connectivity. *Neuroimage* **57**(1), 130–139 (2011). <https://doi.org/10.1016/j.neuroimage.2011.04.010>
- Huang, E.Y.: *Networks of Coupled Oscillators and Social Network Structures of Teams*. University of California, Santa Barbara (2020)
- Hannay, K.M., Forger, D.B., Booth, V.: Macroscopic models for networks of coupled biological oscillators. *Sci. Adv.* **4**(8), 1701047 (2018). <https://doi.org/10.1126/sciadv.1701047>
- Braiman, Y., Lindner, J.F., Ditto, W.L.: Taming spatiotemporal chaos with disorder. *Nature* **378**(6556), 465–467 (1995). <https://doi.org/10.1038/378465a0>
- Wiesenfeld, K.: New results on frequency-locking dynamics of disordered Josephson arrays. *Physica B* **222**(4), 315–319 (1996). [https://doi.org/10.1016/0921-4526\(96\)85057-5](https://doi.org/10.1016/0921-4526(96)85057-5)
- Valizadeh, A., Kolahchi, M., Straley, J.: Single phase-slip junction site can synchronize a parallel superconducting array of linearly coupled Josephson junctions. *Phys. Rev. B* **82**(14), 144520 (2010). <https://doi.org/10.1103/PhysRevB.82.144520>
- Zhang, Y., Wang, C., Tang, J., Ma, J., Ren, G.: Phase coupling synchronization of FHN neurons connected by a Josephson junction. *Sci. China Technol. Sci.* **63**(11), 2328–2338 (2020). <https://doi.org/10.1007/s11431-019-1547-5>
- Zhang, Y., Xu, Y., Yao, Z., Ma, J.: A feasible neuron for estimating the magnetic field effect. *Nonlinear Dyn.* **102**(3), 1849–1867 (2020). <https://doi.org/10.1007/s11071-020-05991-y>
- Zhou, P., Yao, Z., Ma, J., Zhu, Z.: A piezoelectric sensing neuron and resonance synchronization between auditory neurons under stimulus. *Chaos Solitons Fractals* **145**, 110751 (2021). <https://doi.org/10.1016/j.chaos.2021.110751>

24. Mirollo, R.E., Strogatz, S.H.: Synchronization of pulse-coupled biological oscillators. *SIAM J. Appl. Math.* **50**(6), 1645–1662 (1990). <https://doi.org/10.1137/0150098>
25. Hansel, D., Mato, G., Meunier, C.: Synchrony in excitatory neural networks. *Neural Comput.* **7**(2), 307–337 (1995). <https://doi.org/10.1162/neco.1995.7.2.307>
26. Ermentrout, B.: Type I membranes, phase resetting curves, and synchrony. *Neural Comput.* **8**(5), 979–1001 (1996). <https://doi.org/10.1162/neco.1996.8.5.979>
27. Van Vreeswijk, C., Abbott, L., Ermentrout, G.: When inhibition not excitation synchronizes neural firing. *J. Comput. Neurosci.* **1**(4), 313–321 (1994). <https://doi.org/10.1007/bf00961879>
28. Ernst, U., Pawelzik, K., Geisel, T.: Synchronization induced by temporal delays in pulse-coupled oscillators. *Phys. Rev. Lett.* **74**, 1570–1573 (1995). <https://doi.org/10.1103/PhysRevLett.74.1570>
29. Ernst, U., Pawelzik, K., Geisel, T.: Delay-induced multistable synchronization of biological oscillators. *Phys. Rev. E* **57**, 2150–2162 (1998). <https://doi.org/10.1103/PhysRevE.57.2150>
30. Sadeghi, S., Valizadeh, A.: Synchronization of delayed coupled neurons in presence of inhomogeneity. *J. Comput. Neurosci.* **36**(1), 55–66 (2014). <https://doi.org/10.1007/s10827-013-0461-9>
31. Esfahani, Z.G., Valizadeh, A.: Zero-lag synchronization despite inhomogeneities in a relay system. *PLoS ONE* **9**(12), 112688 (2014). <https://doi.org/10.1371/journal.pone.0112688>
32. Esfahani, Z.G., Gollo, L.L., Valizadeh, A.: Stimulus-dependent synchronization in delayed-coupled neuronal networks. *Sci. Rep.* **6**(1), 1–10 (2016). <https://doi.org/10.1038/srep23471>
33. Gollo, L.L., Breakspear, M.: The frustrated brain: from dynamics on motifs to communities and networks. *Philos. Trans. Roy. Soc. B Biol. Sci.* **369**(1653), 20130532 (2014). <https://doi.org/10.1098/rstb.2013.0532>
34. Breakspear, M., Heitmann, S., Daffertshofer, A.: Generative models of cortical oscillations: neurobiological implications of the Kuramoto model. *Front. Hum. Neurosci.* **4**, 190 (2010). <https://doi.org/10.3389/fnhum.2010.00190>
35. Villegas, P., Moretti, P., Munoz, M.A.: Frustrated hierarchical synchronization and emergent complexity in the human connectome network. *Sci. Rep.* **4**(1), 1–7 (2014). <https://doi.org/10.1038/srep05990>
36. Levnajić, Z.: Emergent multistability and frustration in phase-repulsive networks of oscillators. *Phys. Rev. E* **84**, 016231 (2011). <https://doi.org/10.1103/PhysRevE.84.016231>
37. Wannier, G.H.: Antiferromagnetism, the triangular Ising net. *Phys. Rev.* **79**, 357–364 (1950). <https://doi.org/10.1103/PhysRev.79.357>
38. Nixon, M., Ronen, E., Friesem, A.A., Davidson, N.: Observing geometric frustration with thousands of coupled lasers. *Phys. Rev. Lett.* **110**, 184102 (2013). <https://doi.org/10.1103/PhysRevLett.110.184102>
39. Baboux, F., Ge, L., Jacqmin, T., Biondi, M., Galopin, E., Lemaître, A., Le Gratiet, L., Sagnes, I., Schmidt, S., Türeci, H.E., Amo, A., Bloch, J.: Bosonic condensation and disorder-induced localization in a flat band. *Phys. Rev. Lett.* **116**, 066402 (2016). <https://doi.org/10.1103/PhysRevLett.116.066402>
40. Yoshimoto, M., Yoshikawa, K., Mori, Y.: Coupling among three chemical oscillators: synchronization, phase death, and frustration. *Phys. Rev. E* **47**, 864–874 (1993). <https://doi.org/10.1103/PhysRevE.47.864>
41. Meiboom, S., Sethna, J.P., Anderson, P.W., Brinkman, W.F.: Theory of the blue phase of cholesteric liquid crystals. *Phys. Rev. Lett.* **46**, 1216–1219 (1981). <https://doi.org/10.1103/PhysRevLett.46.1216>
42. Nelson, D.R.: Order, frustration, and defects in liquids and glasses. *Phys. Rev. B* **28**, 5515–5535 (1983). <https://doi.org/10.1103/PhysRevB.28.5515>
43. Sethna, J.P.: Frustration, curvature, and defect lines in metallic glasses and the cholesteric blue phase. *Phys. Rev. B* **31**, 6278–6297 (1985). <https://doi.org/10.1103/PhysRevB.31.6278>
44. Chaudhari, P., Turnbull, D.: Structure and properties of metallic glasses. *Science* **199**(4324), 11–21 (1978). <https://doi.org/10.1126/science.199.4324.11>
45. Giauque, W., Stout, J.: The entropy of water and the third law of thermodynamics, the heat capacity of ice from 15 to 273° K. *J. Am. Chem. Soc.* **58**(7), 1144–1150 (1936). <https://doi.org/10.1021/ja01298a023>
46. Kang, L., Wang, Z., Huo, S., Tian, C., Liu, Z.: Remote synchronization in human cerebral cortex network with identical oscillators. *Nonlinear Dyn.* **99**(2), 1577–1586 (2020). <https://doi.org/10.1007/s11071-019-05375-x>
47. Ansariara, M., Emadi, S., Adami, V., Botha, A., Kolahchi, M.: Signs of memory in a plastic frustrated Kuramoto model of neurons. *Nonlinear Dyn.* **100**(4), 3685–3694 (2020). <https://doi.org/10.1007/s11071-020-05705-4>
48. Jensen, M.H., Krishna, S., Pigolotti, S.: Repressor lattice: feedback, commensurability, and dynamical frustration. *Phys. Rev. Lett.* **103**, 118101 (2009). <https://doi.org/10.1103/PhysRevLett.103.118101>
49. Sadoc, J.F., Mosseri, R.: *Geometrical Frustration*. Cambridge (1999)
50. Ramires, A.: Frustration can be critical. *Nat. Phys.* **15**(12), 1212–1214 (2019). <https://doi.org/10.1038/s41567-019-0668-4>
51. Yu, R., Mobbs, D., Seymour, B., Rowe, J.B., Calder, A.J.: The neural signature of escalating frustration in humans. *Cortex* **54**, 165–178 (2014). <https://doi.org/10.1016/j.cortex.2014.02.013>
52. Abler, B., Walter, H., Erk, S.: Neural correlates of frustration. *Neuro Rep.* **16**(7), 669–672 (2005). <https://doi.org/10.1097/00001756-200505120-00003>
53. Winfree, A.T.: Biological rhythms and the behavior of populations of coupled oscillators. *J. Theor. Biol.* **16**(1), 15–42 (1967). [https://doi.org/10.1016/0022-5193\(67\)90051-3](https://doi.org/10.1016/0022-5193(67)90051-3)
54. Gallego, R., Montbrió, E., Pazó, D.: Synchronization scenarios in the winfree model of coupled oscillators. *Phys. Rev. E* **96**, 042208 (2017). <https://doi.org/10.1103/PhysRevE.96.042208>
55. Ha, S.Y., Kang, M., Moon, B.: On the emerging asymptotic patterns of the winfree model with frustrations. *Nonlinearity* **34**(4), 2454–2482 (2021). <https://doi.org/10.1088/1361-6544/abb9f8>
56. Kraleman, B., Frühwirth, M., Pikovsky, A., Rosenblum, M., Kenner, T., Schaefer, J., Moser, M.: In vivo cardiac phase

- response curve elucidates human respiratory heart rate variability. *Nat. Commun.* **4**(1), 1–9 (2013). <https://doi.org/10.1038/ncomms3418>
57. Izhikevich, E.M.: *Dynamical Systems in Neuroscience*. MIT Press (2007)
 58. Tsubo, Y., Teramae, J.-N., Fukai, T.: Synchronization of excitatory neurons with strongly heterogeneous phase responses. *Phys. Rev. Lett.* **99**, 228101 (2007). <https://doi.org/10.1103/PhysRevLett.99.228101>
 59. Neltner, L., Hansel, D., Mato, G., Meunier, C.: Synchrony in heterogeneous networks of spiking neurons. *Neural Comput.* **12**(7), 1607–1641 (2000). <https://doi.org/10.1162/089976600300015286>
 60. Goel, P., Ermentrout, B.: Synchrony, stability, and firing patterns in pulse-coupled oscillators. *Physica D* **163**(3–4), 191–216 (2002). [https://doi.org/10.1016/S0167-2789\(01\)00374-8](https://doi.org/10.1016/S0167-2789(01)00374-8)
 61. Schreiber, T.: Measuring information transfer. *Phys. Rev. Lett.* **85**, 461–464 (2000). <https://doi.org/10.1103/PhysRevLett.85.461>
 62. Wibral, M., Rahm, B., Rieder, M., Lindner, M., Vicente, R., Kaiser, J.: Transfer entropy in magnetoencephalographic data: quantifying information flow in cortical and cerebellar networks. *Prog. Biophys. Mol. Biol.* **105**(1–2), 80–97 (2011). <https://doi.org/10.1016/j.pbiomolbio.2010.11.006>
 63. Vicente, R., Wibral, M., Lindner, M., Pipa, G.: Transfer entropy—a model-free measure of effective connectivity for the neurosciences. *J. Comput. Neurosci.* **30**(1), 45–67 (2011). <https://doi.org/10.1007/s10827-010-0262-3>
 64. Vakorin, V.A., Kovacevic, N., McIntosh, A.R.: Exploring transient transfer entropy based on a group-wise ica decomposition of eeg data. *Neuroimage* **49**(2), 1593–1600 (2010). <https://doi.org/10.1016/j.neuroimage.2009.08.027>
 65. Gourévitch, B., Eggermont, J.J.: Evaluating information transfer between auditory cortical neurons. *J. Neurophysiol.* **97**(3), 2533–2543 (2007). <https://doi.org/10.1152/jn.01106.2006>
 66. Montalto, A., Faes, L., Marinazzo, D.: Mute: a matlab toolbox to compare established and novel estimators of the multivariate transfer entropy. *PLoS ONE* **9**(10), 109462 (2014). <https://doi.org/10.1371/journal.pone.0109462>
 67. Bolhasani, E., Azizi, Y., Valizadeh, A.: Direct connections assist neurons to detect correlation in small amplitude noises. *Front. Comput. Neurosci.* **7**, 108 (2013). <https://doi.org/10.3389/fncom.2013.00108>
 68. Bolhasani, E., Azizi, Y., Valizadeh, A., Perc, M.: Synchronization of oscillators through time-shifted common inputs. *Phys. Rev. E* **95**, 032207 (2017). <https://doi.org/10.1103/PhysRevE.95.032207>
 69. Kirst, C., Timme, M., Battaglia, D.: Dynamic information routing in complex networks. *Nat. Commun.* **7**(1), 1–9 (2016). <https://doi.org/10.1038/ncomms11061>
 70. Atallah, B.V., Scanziani, M.: Instantaneous modulation of gamma oscillation frequency by balancing excitation with inhibition. *Neuron* **62**(4), 566–577 (2009). <https://doi.org/10.1016/j.neuron.2009.04.027>
 71. Buzsáki, G., Wang, X.-J.: Mechanisms of gamma oscillations. *Annu. Rev. Neurosci.* **35**, 203 (2012). <https://doi.org/10.1146/annurev-neuro-062111-150444>
 72. Malagurski, B., Deschwanden, P.F., Jäncke, L., Mérillat, S.: Longitudinal functional connectivity patterns of the default mode network in healthy older adults. *NeuroImage* (2022). <https://doi.org/10.1016/j.neuroimage.2022.119414>
 73. Damoiseaux, J.S., Greicius, M.D.: Greater than the sum of its parts: a review of studies combining structural connectivity and resting-state functional connectivity. *Brain Struct. Funct.* **213**(6), 525–533 (2009). <https://doi.org/10.1007/s00429-009-0208-6>
 74. Rabinovich, M., Huerta, R., Laurent, G.: Transient dynamics for neural processing. *Science (New York, N.Y.)* **321**(5885), 48–50 (2008)
 75. Deco, G., Jirsa, V., McIntosh, A.R., Sporns, O., Kötter, R.: Key role of coupling, delay, and noise in resting brain fluctuations. *Proc. Natl. Acad. Sci.* **106**(25), 10302–10307 (2009). <https://doi.org/10.1073/pnas.090183110>
 76. Deco, G., Jirsa, V.K., McIntosh, A.R.: Emerging concepts for the dynamical organization of resting-state activity in the brain. *Nat. Rev. Neurosci.* **12**(1), 43–56 (2011). <https://doi.org/10.1038/nrn2961>
 77. Ghosh, A., Rho, Y., McIntosh, A.R., Kötter, R., Jirsa, V.K.: Noise during rest enables the exploration of the brain’s dynamic repertoire. *PLoS Comput. Biol.* **4**(10), 1000196 (2008). <https://doi.org/10.1371/journal.pcbi.1000196>
 78. Honey, C.J., Kotter, R., Breakspear, M., Sporns, O.: Network structure of cerebral cortex shapes functional connectivity on multiple time scales. *Proc. Natl. Acad. Sci.* **104**(24), 10240–10245 (2007). <https://doi.org/10.1073/pnas.0701519104>
 79. Toulouse, G.: Theory of the frustration effect in spin glasses: I. Spin Glass Theory and Beyond: An Introduction to the Replica Method and Its Applications, vol. 9, p. 99 (1987)
 80. Van Hemmen, J., Wreszinski, W.: Lyapunov function for the kuramoto model of nonlinearly coupled oscillators. *J. Stat. Phys.* **72**(1), 145–166 (1993). <https://doi.org/10.1007/BF01048044>
 81. Friston, K.: The free-energy principle: a unified brain theory? *Nat. Rev. Neurosci.* **11**(2), 127–138 (2010). <https://doi.org/10.1038/nrn2787>
 82. Friston, K., Kiebel, S.: Predictive coding under the free-energy principle. *Philos. Trans. Roy. Soc. B Biol. Sci.* **364**(1521), 1211–1221 (2009). <https://doi.org/10.1098/rstb.2008.0300>

Publisher’s Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.