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Chimeras in Physics and Biology: Synchronization and Desynchronization of Rhythms

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Das Video zum Vortrag ist verfügbar unter https://doi.org/10.26164/leopoldina_10_00292.

Abstract

Rhythms influence our life in various ways, e.g., through heart beat and respiration, oscillating brain currents, life cycles and seasons, clocks and metronomes, pulsating lasers, transmission of data packets, and many others. The physics of complex nonlinear systems has developed methods to describe and analyze periodic oscillations and their synchronization in complex networks, which are composed of many components. Synchronized oscillations as well as completely asynchronous chaotic oscillations play a major role in many networks in nature and technology. For instance, the synchronous firing of all neurons in the brain represents a pathological state, like in epilepsy or Parkinson's disease, and should be suppressed, as well as the synchronous mechanical vibration of bridges. On the other hand, synchronization is desirable for the stable operation of power grids or in encrypted communication with chaotic signals. In networks composed of identical components, intriguing hybrid states ("chimeras") may form spontaneously, which consist of spatially coexisting synchronized and desynchronized domains, i.e., seemingly incongruous parts. This might be of relevance in inducing and terminating epileptic seizures, or in unihemispheric sleep which is found in certain migratory birds and mammals, or in cascading failures of the power grid.

Zusammenfassung

Rhythmen prägen unser Leben auf vielfältige Weise, z. B. durch Herzschlag und Atmung, oszillierende Gehirnströme, Lebenszyklen und Jahreszeiten, Uhren und Metronome, pulsierende Laser, Übertragung von Datenpaketen, und vieles andere. Die Physik komplexer nichtlinearer Systeme hat Methoden entwickelt, wie periodische Schwingungen und deren Synchronisation in komplexen Netzwerken, die aus vielen Bestandteilen zusammengesetzt sind, beschrieben und analysiert werden können. Synchronisierte Oszillationen, aber auch völlig desynchronisierte, chaotische Oszillationen spielen eine große Rolle in vielen Netzwerken in Natur und Technik. Beispielsweise ist das synchronisierte Feuern aller Neuronen im Gehirn ein pathologischer Zustand, etwa bei Epilepsie oder Parkinson-Erkrankung, und sollte unterdrückt werden, wie auch synchrone mechanische Schwingungen von Brücken. Andererseits ist die Synchronisation erwünscht beim stabilen Betrieb von Stromnetzen oder bei der verschlüsselten Kommunikation mit chaotischen Signalen. In Netzwerken aus identischen Komponenten können sich überraschenderweise auch spontan Hybrid-Zustände („Schimären") bilden, die aus räumlich koexistierenden synchronisierten und desynchronisierten Bereichen bestehen, welche scheinbar nicht zusammen passen. Diese könnten relevant sein bei der Auslösung oder Beendigung epileptischer Anfälle, oder beim halbseitigen Schlaf einer Gehirnhälfte, der bei bestimmten Zugvögeln oder Säugetieren auftritt, oder beim kaskadenartigen Zusammenbruch des Stromnetzes.

1. Synchronization of Rhythms in Complex Networks

Synchronization phenomena in nonlinear dynamical systems (Haken 1983, Pikovsky et al. 2001, Mosekilde et al. 2002, Haken 2008, Balanov et al. 2009, Schöll et al. 2016, Boccaletti et al. 2018) are of great importance in many areas ranging from physics and chemistry to biology, neuroscience, socio-economic systems, and engineering. Probably the first example was given by Christiaan Huygens (1629–1695), who observed that while two individual pendulum clocks show slightly deviating times, they spontaneously synchronize at exactly the same frequency if they are weakly coupled via a wooden beam (Fig. 1). Even if individual systems, e.g., semiconductor lasers, exhibit chaotic dynamics, they may spontaneously synchronize their chaotic time series if coupled (Soriano et al. 2013).

Fig. 1 Christiaan Huygens (1671) and his sketch of the two coupled pendulum clocks which he observed to synchronize spontaneously. (After Huygens 1932.)

Synchronization of rhythms is also observed generally if more than two oscillating elements are coupled in a network, even for large and complex networks. Complex networks are a ubiquitous paradigm in nature and technology, and a central issue in nonlinear science with applications to different fields ranging from natural to technological and socio-economic systems (Fig. 2). The interplay of nonlinear dynamics, network topology, naturally arising delays, and random fluctuations results in a plethora of spatio-temporal patterns (Schöll et al. 2016).

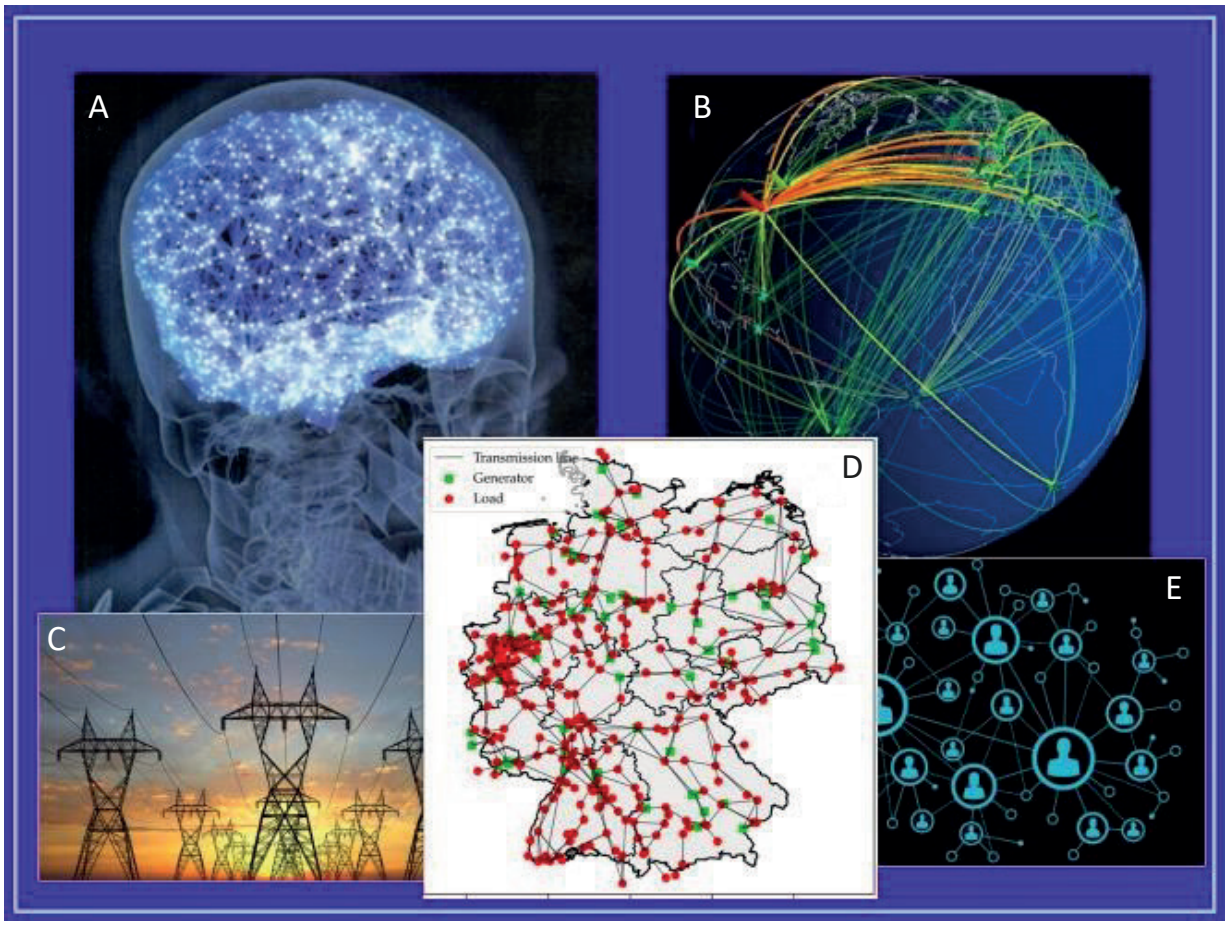

Fig. 2 Complex networks exist in many diverse fields: (*A*) brain, (*B*) internet, (*C*), (*D*) power grids (panel *D* shows the high-voltage power grid of Germany [Taher et al. 2019]), (*E*) social network.

There exist many applications of synchronization in various nonlinear systems, and sometimes synchrony is desirable, whereas sometimes it may be undesirable. Synchronization of lasers with chaotic dynamics, for instance, may lead to new secure communication schemes (Cuomo and Oppenheim 1993, Boccaletti et al. 2002, Argyris et al. 2005, Kanter et al. 2008). The London Millenium Bridge was opened in the year 2000, but had to be closed on the same day, after pedestrians experienced an alarming lateral swaying motion, and it took almost two years while modifications and repairs were made to keep the bridge stable. The instability was explained by a simple network model leading to spontaneous collective crowd synchronization at a critical density of the pedestrians streaming onto the bridge (Strogatz et al. 2005). Synchronization of power grids to the nominal frequency of 50 Hz is essential

for their stable operation (Motter et al. 2013, Tumash et al. 2019, Taher et al. 2019). The synchronization of neurons (Vicente et al. 2008) is believed to play a crucial role in the brain under normal conditions, for instance in the context of memory, cognition and learning (Singer 1999), and under pathological conditions such as Parkinson's disease (Tass et al. 1998) or epilepsy (Andrzejak et al. 2006, Jiruska et al. 2013, Jirsa et al. 2014). Fireflies are known to synchronize their flashing (Buck and Buck 1968). Especially in biology, rhythms and biological clocks play an important role and have given the name to a whole discipline, namely chronobiology (Peschke 2011), see also the Abstracts by Jessica Grahn, Steve Kay, and Russell Foster, in this Meeting. Examples are the circadian rhythms in single-cell organisms, plants, fruit flies, mammals, and humans; the high relevance of chronobiology is documented by the award of the 2017 Nobel Prize for Physiology or Medicine to Jeffrey C. Hall, Michael Rosbash, and Michael W. Young for their discoveries of molecular mechanisms controlling the circadian rhythm.

In many realistic dynamical networks time delay effects are a key issue (Just et al. 2010, Flunkert et al. 2013, Schöll 2013). For example, the finite propagation time of light between coupled semiconductor lasers (Wünsche et al. 2005, Carr et al. 2006, Erzgräber et al. 2006, Fischer et al. 2006, D'Huys et al. 2008, Soriano et al. 2013) significantly influences the dynamics on networks. Similar effects occur in neuronal (Rossoni et al. 2005, Masoller et al. 2008, Schöll et al. 2009) and biological gene expression networks (Tiana and Jensen 2013) due to signal processing and propagation delays. Time delay has two complementary, counterintuitive and almost contradicting facets. On the one hand, delay is able to induce instabilities, generate new dynamical behavior, e.g. periodic and quasiperiodic time evolution, multistability and chaotic motion. On the other hand, delay can suppress instabilities, stabilize unstable stationary or periodic states and may control deterministic chaos. Both facets open up efficient methods of designing and controlling nonlinear dynamics by time-delayed feedback (Schöll and Schuster 2008, Sun and Ding 2013).

There exist different forms of synchronization, i.e., complete or isochronous (zerolag) synchronization, generalized synchronization (where the oscillations of the individual elements of the network are not identical, but functionally related), phase synchronization (where only the phases but not the amplitudes of the oscillations are synchronized), cluster or group synchronization (Sorrentino and Ott 2007, Dahms et al. 2012, Williams et al. 2013, Taylor et al. 2011, Nkomo et al. 2013) (where within each cluster all elements are completely synchronized, but between the clusters there is a phase lag), and many other forms. Some progress has been made in generalizing this work, for instance, towards adaptive networks (Lehnert et al. 2014, Kasatkin et al. 2017, Berner et al. 2019a, b, 2020) (where the strength of the links is adapted dynamically), inhomogeneous local dynamics (Sorrentino and Pecora 2016) and heterogeneous delay times (Cakan et al., 2014), distributed (Kyrychko et al. 2014, Wille et al. 2014), state-dependent, or time-varying delays (Gjurchinovski et al. 2014). In general, the stability of synchronization in delay-coupled networks of oscillators depends in a complicated way on the local dynamics of the nodes and the coupling topology. However, for large coupling delays synchronizability relates in a simple way to the spectral properties of the network topology, characterized by the eigenvalue spectrum of the coupling matrix. The master stability function (Pecora and Carroll 1998) used to determine the stability of synchronous solutions has a universal structure in the limit of large delay: it is rotationally symmetric and monotonically increasing. This allows for a universal classification of networks with respect to synchronization properties (Flunkert et al. 2010). For smaller

coupling delays the synchronization properties depend in a more subtle way upon the local dynamics, and the details of the network topology. Various cluster synchronization states, where certain clusters inside the network show isochronous synchronization, can be realized by tuning the coupling parameters, i.e., the coupling constant which is a complex number with an amplitude (coupling strength) and a phase (coupling phase), and the coupling delay which describes the propagation time of the signals coming from the other nodes (Choe et al. 2010, Dahms et al. 2012). To find appropriate values of these control parameters, the speed-gradient method from control theory can be applied to achieve a desired state of generalized synchrony (*adaptive synchronization*) (Selivanov et al. 2012). Transitions between synchronization and desynchronization can be induced by introducing inhibitory links into an excitable regular network with a probability p in a small-world like fashion, and changing the balance between excitatory and inhibitory links (Lehnert et al. 2011, Keane et al. 2012). Here inhibitory means that the individual element is inhibited by the coupling from the other elements of the network, i.e., the coupling term has a negative sign, whereas excitatory means that the coupling term has a positive sign.

2. Partial Synchronization and Chimera States

Recent research interest has focussed on more complex partial synchronization patterns, where the whole system is not completely in synchrony, but only parts of it have the same phase and frequency. These synchronization patterns may include clusters of self-sustained synchronized oscillations with different phase between the clusters, or desynchronized parts, or other parts where the oscillations are quenched (oscillation death or amplitude death).

An intriguing example of partial synchronization patterns, which has recently gained much attention, are *chimera states*, i.e., symmetry-breaking states of partially coherent and partially incoherent behavior. Chimera states in dynamical networks consist of spatially separated, coexisting domains of synchronized (spatially coherent) and desynchronized (spatially incoherent) dynamics. They are a manifestation of spontaneous symmetry-breaking in systems of identical oscillators, and occur in a variety of physical, chemical, biological, neuronal, ecological, technological, or socio-economic systems. A schematic representation is given in Figure 3, which shows a snapshot in time of the state variable, e.g., the oscillator phase, versus the space variable which labels the different oscillators of the network, e.g., their position on a ring network, for three different dynamical states. In the left panel, all oscillators are synchronized, i.e., they have the same phase (coherence). In the right panel, all oscillators are desynchronized, i.e., neighboring oscillators have completely random phases (incoherence). In the middle panel, a chimera state is depicted which consists of a central domain of desynchronization and a surrounding domain of synchronization. Since the space position is marked on a ring network, the left and the right border of the panel correspond to the same position, i.e., they coincide.

Kuramoto and co-workers discovered the chimeras in a ring network of phase oscillators with a simple symmetric non-local coupling scheme (Kuramoto and Battogtokh 2002). Within these "classical" chimera states, coherent domains of periodic in-phase oscillations coexist with incoherent domains, characterized by chaotic behavior in time and space. In Greek mythology, the chimera is a fire-breathing mythical creature with a lion's, a goat's, and a snake's head. The middle inset of Figure 3 shows the Etruscan Chimera di Arezzo (400 BC),

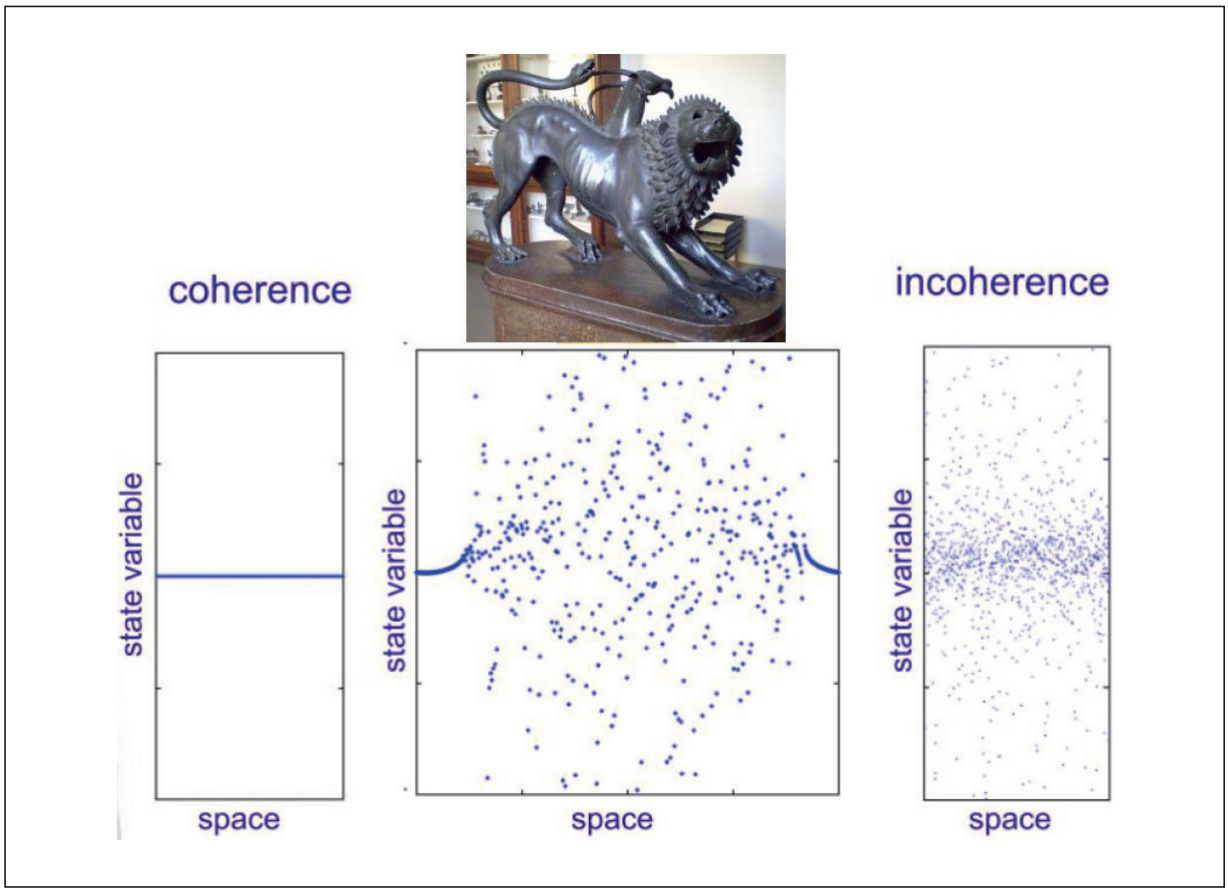

Fig. 3 Scenario from coherence to incoherence: Schematic sketch of snapshot of a chimera state (*middle panel*) compared to completely synchronized (coherent) state (*left panel*) and completely desynchronized (incoherent) state (*right panel*). The state variable, e.g., oscillator phase, is shown *versus* space (position of the oscillators). In the *middle panel* the widely dispersed dots in the center correspond to the desynchronized domain, while the solid lines at the edges correspond to the synchronized domain of the chimera. Due to periodic boundary conditions on a ring network, the left and the right border of each panel correspond to the same position on the ring. The inset shows the Chimera di Arezzo (400 BC) from the National Archeological Museum in Florence, which gave the name to chimera states.

on display in the National Archeological Museum in Florence. As the counterintuitive dynamical chimera state is also composed of incongruous parts, it was named after the beast by Abrams and Strogatz (2004). Kuramoto's finding initiated a broad wave of theoretical and numerical investigations (Motter 2010, Panaggio and Abrams 2015, Schöll et al. 2020). However, only one decade after their theoretical discovery in computer simulations were the first lab experiments on chimeras reported simultaneously in optical light modulators (Hagerstrom et al. 2012) and chemical oscillators (Tinsley et al. 2012), followed by experiments with mechanical (Martens et al. 2013, Kapitaniak et al. 2014), electronic or optoelectronic oscillators (Larger et al. 2013, 2015), electrochemical systems (Wickramasinghe and Kiss 2013, 2014, Schmidt et al. 2014), and electronic circuits (Gambuzza et al. 2014, Rosin et al. 2014). Theoretical studies have found chimeras also in various other systems and for complex topologies. These include time-discrete maps (Omelchenko et al. 2011, Semenova et al. 2015) and time-continuous chaotic models (Omelchenko et al. 2012), and Boolean networks (Rosin et al. 2014). Chimeras were found in a variety of different dynamic models: the Stuart-Landau model (Zakharova et al. 2014), the Van-der-Pol oscillator (Omelchenko et al.

2015b), the FitzHugh-Nagumo neural model (Omelchenko et al. 2013, 2015a), and systems of type-I excitability (Vüllings et al. 2014), as well as in globally coupled lasers (Böhm et al. 2015), in population dynamics (Hizanidis et al. 2015, Banerjee et al. 2016), and in quantum oscillator systems (Bastidas et al. 2015). In real-world systems chimera states might play a role, e.g., in power grids (Motter et al. 2013), in social systems (Gonzalez-Avella et al. 2014), or in the unihemispheric sleep of birds and dolphins (Rattenborg et al. 2000, 2016), where some migratory birds and sea mammals sleep with one half of their brain, while the other half remains awake, and the two hemispheres switch spontaneously, and in epileptic seizures (Rothkegel and Lehnertz 2014, Andrzejak et al. 2016), which are characterized by excessive synchrony and may be initiated or terminated by transient brain states of partial high synchronization, i.e. chimeras.

Usually, both the chimera state and the completely synchronized state are stable for perturbations within a certain neighborhood region in phase space, which is called the basin of attraction of the respective state. Typically, the basin of attraction of the chimera state is relatively small compared to that of the synchronized state. This explains why they were not detected for a long time. By choosing appropriate initial conditions, one can secure that the system is asymptotically attracted to the chimera state and not to the completely synchronized state. An interesting feature of the chimera states is that they are often long living transients towards the in-phase synchronized oscillatory state. By this, the coupling between the oscillators introduces a time scale much larger than the oscillation periods of each single oscillator. It was theoretically predicted (Wolfrum and Omel'chenko 2011) and experimentally confirmed (Rosin et al. 2014) that the lifetime of the chimera states of phase oscillators grows exponentially with the system size. This illustrates impressively that they are not simply a temporary trace of the initial conditions, but are a persisting phenomenon.

Recently, the investigation of chimera states has been generalized towards networks of elements which have more complicated local dynamics (Panaggio and Abrams 2015, Böhm et al. 2015, Omelchenko et al. 2015b). In particular, nodes which involve not only phase but also amplitude dynamics are considered. As described in Sethia et al. (2013) and Sethia and Sen (2014), in such systems amplitude-mediated chimeras can be found, which show a chimera behavior with respect to the phases as well as with respect to the amplitudes. Another type of chimera states is characterized by strictly correlated phase dynamics throughout the whole network, but coexisting domains of coherent and incoherent amplitude dynamics. These *amplitude chimeras* were first described in ring networks by Zakharova et al. (2014). A crucial difference to classical phase chimeras is that the spatial incoherence does not imply chaotic behavior in time. In fact, all nodes of an amplitude chimera perform periodic oscillations, but in the incoherent domain the spatial sequence of the positions of the centers of oscillation is completely random. It has been noted (Tumash et al. 2017) that amplitude chimeras are long living transients, and their lifetime and their robustness with respect to noise was investigated in detail in Loos et al. (2016). It has been shown that the chimera lifetime can be effectively tuned by adding a simple symmetric proportional control term (Sieber et al. 2014), and that the chimera position can be stabilized by an asymmetric feedback loop (Bick and Martens 2015). Both control schemes have been combined in a double-feedback control which is composed of two parts, a symmetric and an asymmetric one (Omelchenko et al. 2016). Since this is, in an abstract sense, similar to the two levers of a pair of tweezers, it has been named *tweezer control* and it was shown to be able to stabilize chimeras in very small networks (Omelchenko et al. 2016, 2018, 2019). Noise-induced chimera effects like

stochastic resonance of chimeras (Semenov et al. 2016) or coherence resonance chimeras (Semenova et al. 2016) have also been studied.

An important extension of the topology are multilayer networks where the nodes are distributed in different layers. One of the most promising applications of the multilayer approach is the study of the brain, where the neurons can form different layers. A special case of multilayer networks are multiplex topologies, where each layer contains the same set of nodes, and only pairwise connections between corresponding nodes from neighbouring layers exist. In particular, remote (or relay) synchronization in multilayer networks between parts of one layer and their counterparts in a second layer, where these two layers are not directly connected, has recently provoked much interest (Leyva et al. 2018). A simple realization of such a system is a triplex network where a relay layer in the middle, which is generally not synchronized, acts as a transmitter between two outer layers. It has been shown that the three-layer structure of the network allows for synchronization of the coherent domains of chimera states in the first layer with their counterparts in the third layer, whereas the incoherent domains either remain desynchronized or synchronized (Sawicki et al. 2018). In neuroscience various scenarios have been uncovered where specific brain areas act as a functional relay between other brain regions, having a strong influence on signal propagation, brain functionality, and dysfunctions (Roelfsema et al. 1997, Soteropoulos and Baker 2006). For instance, the relay cells of the thalamus serve both as the primary relay of sensory information from the periphery to the cortex and as an interactive hub of communication between cortical areas (Sherman 2016, Rhodes and Llinas 2005, Guillery and Sherman 2002, Gollo et al. 2010). They enable visual processing (Wang et al. 2011) and rapid coordination of spatially segregated cortical computations important for cognitive flexibility, cognitive control and its perturbation in disease states (Halassa and Kastner 2017). Parahippocampal regions can be considered as relay stations, which actively gate impulse traffic between neocortex and hippocampus, with strong implications for the propagation of neural activity (de Curtis and Paré 2004]. The hippocampus also acts as a relay in the cortico-cortical theta synchronization (Fischer et al. 2006, Gollo et al. 2011); signal transmission between cortical and subcortical brain regions is involved in a wide range of brain functions (Prasad and Chudasama 2013). Especially partial relay synchronization plays an important role in experiments with mice (Gollo et al. 2011), where just a part of the hippocampal relay exhibits phase-lag synchronization with the two cortical regions, which between themselves exhibit partial zero-lag synchronization. The computer simulations (Sawicki et al. 2018) might help in elucidating complex scenarios of information processing in the brain, and explain hitherto unexplained experiments on imperfect synchronization in the mice brain (Gollo et al. 2011) by novel scenarios of partial relay inter-layer synchronization.

3. Application to Neurodynamics

Neuroscience offers important applications for chimera states, as mentioned above. Here we review recent computer simulations of chimera states in neuronal networks of FitzHugh-Nagumo (FHN) oscillators (FitzHugh 1961, Nagumo et al. 1962) with a particular emphasis on complex network topologies. The FHN system is a paradigmatic model of excitable dynamics, whose relevance is not limited to neuroscience, but also includes chemical (Shima and Kuramoto 2004) and optoelectronic (Rosin et al. 2011) oscillators and nonlinear electronic

circuits (Heinrich et al. 2010). Excitable dynamics is characterized by a stable steady state, from which the system can be excited by a sufficiently large perturbation which takes the system across a threshold and leads to the emission of a single spike before returning to the stable steady state (recovery phase). Note that while the FHN model was originally invented to describe a single neuron in terms of the membrane potential u and the recovery variable v which models the negative linear feedback leading to recovery after electrical excitation, it is also often used as a generic model for excitable media on a coarse-grained level. The FHN model then describes neural areas by two simple differential equations for an activator variable (the membrane potential) and an inhibitor variable (recovery variable). Usually, the activator exhibits fast dynamics, while the inhibitor displays slow dynamics.

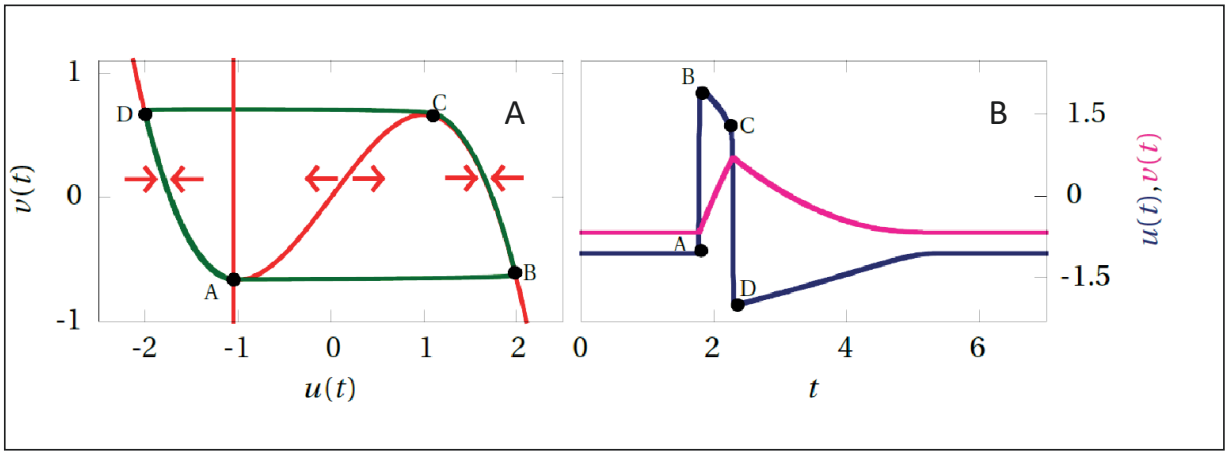

Fig. 4 Intuitive illustration of the FitzHugh-Nagumo (FHN) model of excitable dynamics. (*A*) Phase portrait of the activator variable $u(t)$ versus the inhibitor variable $v(t)$. The stable steady state (point A) is given by the intersection of the red vertical line and the red curve (graph of a cubic function). The red arrows schematically indicate the dynamic flow, i.e., the fast temporal dynamics in the phase plane ($u(t)$, $v(t)$). A sufficiently strong perturbation from the steady state A takes the system along the green line fast to point B, then slowly along the red cubic curve to point C (excitation phase), then fast to point D, and finally the system slowly returns to the steady state A. (*B*) Corresponding excitation pulse A-B-C-D of the activator variable $u(t)$ (blue) *versus* time t. The magenta time trace shows the associated inhibitor variable $v(t)$.

An intuitive understanding of excitable dynamics can be gained from Figure 4. In the excitable regime, the activator variable shows a rapid increase (activation of the membrane potential) from A to B, initiating an excitation pulse, lasting up to point B, while the inhibitor inhibits the increase of the activator and leads back via C and D to the stable steady state A (green cycle in Fig. 4*A*). Thus, upon sufficiently strong perturbation, exactly one electrical pulse is emitted (blue trace in Fig. 4*B*). Here we consider a network of N coupled FHN oscillators (Omelchenko et al. 2013, 2015a) where u_k and v_k, $k = 1, ..., N$ are the activator and inhibitor variables, respectively. For the mathematical description via a system of $2N$ ordinary differential equations see Appendix A. The important feature is that the equations contain not only direct u–u and v–v couplings, but also cross-couplings between activator (u) and inhibitor (v) variables, and that the coupling between the oscillators is not only to the nearest neighbors, but also to some more distant nodes of the network.

First, we consider a one-dimensional ring topology of N nonlocally coupled FHN oscillators, where each element is coupled to R neighbors on either side (Omelchenko et al. 2013).

It is convenient to consider the ratio $r = R/N$, called coupling radius, which ranges from $1/N$ (nearest-neighbor coupling) to 0.5 (all-to-all coupling). The form of the coupling is inspired from neuroscience, where strong interconnections between different neural areas are often found within a range R, but fewer connections exist at longer distances. We approximate this feature by constant coupling with a strength $\sigma > 0$ within the R nearest neighbors from both sides, and vanishing coupling at longer distances. As shown in Omel'chenko et al. (2010) und Omelchenko et al. (2013), chimera states can be generically found if the activator-inhibitor cross-coupling is much stronger than the direct activator-activator and inhibitor-inhibitor coupling. Figure 5(*A*) shows a snapshot of the variables u_k at time $t = 5000$. One can clearly distinguish coherent and incoherent parts, a characteristic signature of chimera states. Elements that belong to the incoherent part are scattered along the red cycle (see Fig. 5*B*), which is similar to the green cycle of a single FHN oscillator (in Fig. 4*A*). The subsystems of this region perform a nonuniform rotational motion, but neighboring oscillators are not phase-locked. To illustrate this, Figure 5(*C*) shows the mean phase velocities for each oscillator calculated as $\omega_k = 2\pi M_k/\Delta T$, $k = 1, ..., N$, where M_k is the number of complete rotations along the cycle performed by the k-th oscillator during the time interval ΔT. The values of ω_k lie on a continuous curve and the interval of constant ω_k corresponds to the coherent region, where neighboring elements are phase-locked. This phase velocity profile is a clear indication of chimera states and similar to the case of coupled phase oscillators (Kuramoto and Battogtokh 2002, Abrams and Strogatz 2004).

The spatial coherence and incoherence of the chimera state can be characterized by a real-valued local order parameter (Wolfrum et al. 2011, Omelchenko et al. 2011) which measures the degree of synchrony. It is close to one if neighboring oscillators are in synchrony (coherent domain of the chimera), and less than one if they are not (incoherent domain of the chimera). Figure 5(*D*) depicts the local order parameter in the time interval $t \in [1000, 5000]$, where bright yellow color denotes the coherent regions, and dark blue indicates the incoherent domain of the chimera.

Next, we consider fractal network topologies (Omelchenko et al. 2015a). The study of different fractal architectures in the neuron connectivity is motivated by magnetic resonance imaging (MRI) results of the brain structure which show that the network comprising the axons of the neurons spans the brain area fractally and not homogeneously (Katsaloulis et al. 2009, Expert et al. 2011, Katsaloulis et al. 2012). In the remainder of this section the word 'fractal' will be employed to denote mainly hierarchical structures of finite orders n, since the human brain has finite size and does not cover all orders, $n \to \infty$ (as in the exact definition of a fractal set). The fractal connectivity dictates a hierarchical ordering in the distribution of neurons which is essential for the fast and optimal handling of information in the brain.

Simple one-dimensional fractal structures can be constructed using the classic Cantor construction process (Fig. 6). Starting with a base pattern (initiation string) containing b symbols (0's or 1's) we iterate it n times and thus obtain systems of size $N = b^n$. By closing this string b^n of symbols in a ring we construct a hierarchical connectivity matrix considering that the symbol 1 denotes the existence of a link, while the symbol "0" denotes the absence of a link.

In this way a connectivity matrix of size $N = b^n$ is constructed, which contains a hierarchical distribution of gaps with a variety of sizes. The number of times the symbol "1" appears in the base pattern, denoted by c_1, defines formally the fractal dimension d_f of the structure, as $d_f = \ln c_1/\ln b$. This measure d_f describes perfectly the fractal structure when the number of iterations $n \to \infty$. The construction of the fractal connectivity is illustrated in Figure 6 for the

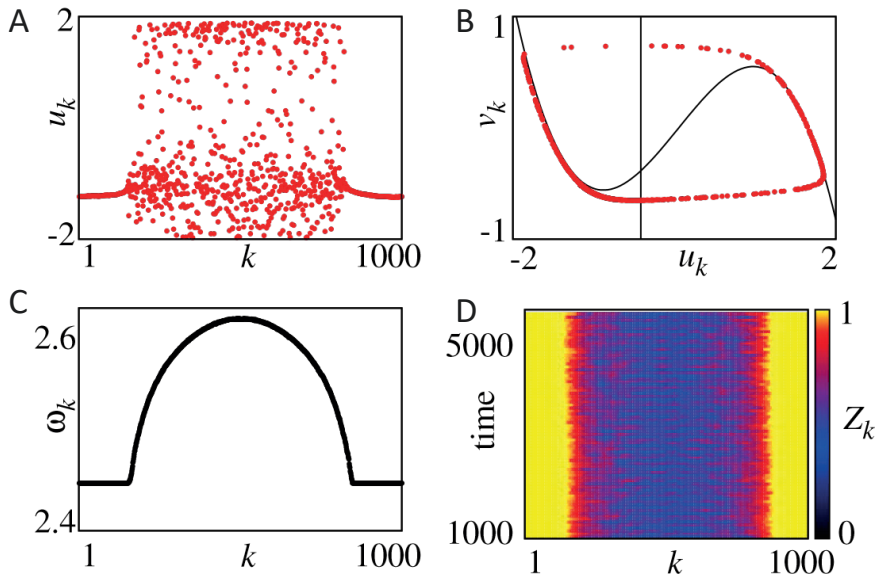

Fig. 5 Computer simulation of a chimera state: (*A*) Snapshot of the activator variables u_k for $t = 5000$, (*B*) snapshot in the (u_k, v_k)-plane for $t = 5000$ (black lines correspond to the red curves in Fig.4a, called *nullclines*), (*C*) mean phase velocities ω_k, (*D*) local order parameter Z_k. Parameters: $N = 1000$, $\varepsilon = 0.05$, $a = 0.5$, $r = 0.35$, $\sigma = 0.1$, $\varphi = \pi/2-0.1$. Initial conditions are randomly distributed on the circle $u^2 + v^2 = 4$. (After Omelchenko et al. 2013).

simple case $b = 3$ and $n = 3$ with the base pattern 101. In the following computer simulations in Fig. 7 we use more complex base patterns with $b = 6$ and $n = 4$ giving a total size of the network $N = b^4 = 1296$ nodes.

In Figure 7(*A*) the calculations are performed with $c_1 = 3$. The connectivity matrix is very sparse and has a fractal dimension $d_f = \ln 3/\ln 6 = 0.6132$. In the $n = 4$ iteration it contains only $c_1^n = 3^4 = 81$ links of each element with the others, each element failing to link with the remaining $b^n - c_1^n = 1215$ elements. The links are mostly isolated while the gaps cover most of the structure. A multi-chimera with multiplicity 8 and clearly identified coherent/incoherent parts is observed. This result agrees with previously published works indicating that the multiplicity of a chimera state is high when the number of links in the ring network is small (Omelchenko et al. 2013, Zakharova et al. 2014, Omelchenko et al. 2015b).

In Figure 7(*B*) the number of links is increased to $c_1 = 4$. The connectivity matrix has a fractal dimension $d_f = \ln 4/\ln 6 = 0.7737$ and each element is connected to $c_1^n = 256$ others. Here, the chimera represents a nested structure, containing 10 coherent/incoherent regions clustered into two parts. The two incoherent parts show a substructure consisting of five closely packed incoherent regions. The two clusters are separated by large coherent regions. In Figure 7(*C*) we consider the value of $c_1 = 5$. Now each element is coupled with $c_1^n = 5^4 = 625$ elements. The incoherent parts seem to merge into a 1-chimera, but the calculation of the phase velocity demonstrates that this single incoherent region has a substructure with three maxima. In conclusion, for a hierarchical topology the chimera state shows nested complex incoherent patterns. Similar chimera patterns have also been found in models using other types of dynamics than the FitzHugh-Nagumo model (Hizanidis et al. 2015, Tsigkri-DeSmedt et al. 2017, Ulonska et al. 2016, Sawicki et al. 2017).

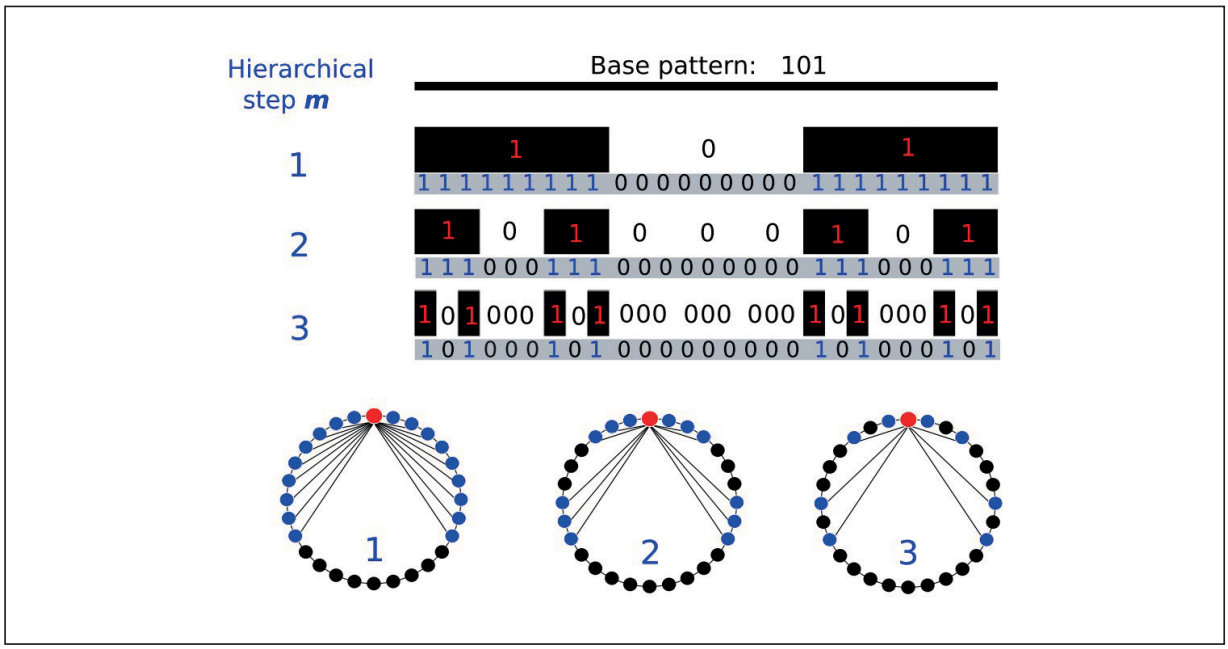

Fig. 6 Construction of the fractal network connectivity for $b = 3$, $n = 3$ with the base pattern 101, and hierarchical steps $m = 1, 2, 3$. Black blocks highlight the symbols **1**, which are replaced by the base pattern in the next iteration; the symbols **0** are replaced by blocks of **0** of the corresponding base pattern length (three in the present case). Light gray panels show the corresponding row of the adjacency matrix for each hierarchical step, excluding the first (reference) node. The bottom panel depicts the obtained coupling schemes for $m = 1, 2, 3$. The reference node is marked red, it is coupled to nodes marked blue. The scheme is valid for each node of the network, correspondingly. Note the systematic dilution of the connectivity with increasing hierarchical step. (After zur Bonsen et al. 2018).

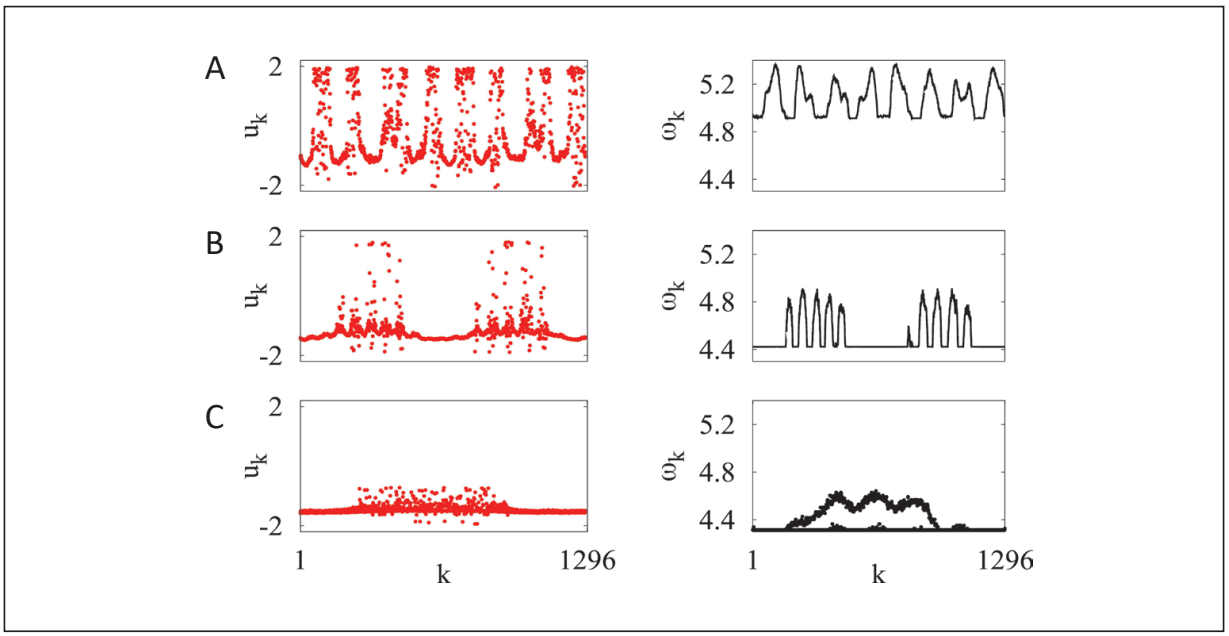

Fig. 7 Computer simulation of a chimera state with fractal connectivities: Snapshots of the activator variable u_k (*left column*) and corresponding mean phase velocities ω_k (*right column*) for different fractal connectivity matrices. The fractal dimensions of the connectivity structures are: (A) $d_f = \ln 3/\ln 6 = 0.6132$ (base pattern: 100101), (B) $d_f = \ln 4/\ln 6 = 0.7737$ (base pattern: 101110) and (C) $d_f = \ln 5/\ln 6 = 0.8982$ (base pattern: 110111). Parameters: $N = 6^4 = 1296$, $\sigma = 0.3$ and other parameters as in Fig. 5. (After Omelchenko et al. 2015a.)

4. Simulation of Epileptic Seizures

In this section, we apply the FitzHugh-Nagumo model to simulate epileptic seizures (Chouzouris et al. 2018). During an epileptic seizure the electrical activity in the brain is excessive and synchronous, and studying chimera states can give further insight into the underlying mechanisms of the initiation or termination of epileptic seizures. We simulate the transition from asynchronous behaviour (healthy state) to synchrony (epileptic seizure) via chimera states for an empirical structural brain network, which has some similarity with a mathematically constructed network with two-dimensional modular fractal connectivity (Krishnagopal et al. 2017). To describe the dynamics of individual units, we use the paradigmatic FitzHugh-Nagumo oscillator as in the previous section. The empirical structural neural connectivity A_{kj} was obtained from diffusion-weighted magnetic resonance imaging data (Melicher et al. 2015) measured in a human brain divided into 90 cortical and subcortical regions according to the Automated Anatomical Labelling (AAL) atlas (Tzourio-Mazoyer et al. 2002), each region corresponding to a node in the network. To provide insight into the nature of the real brain connectivities we have also compared our computer simulations with an artificial connectivity matrix constructed by a well-defined iterative mathematical algorithm generating a two-dimensional modular fractal connectivity (Chouzouris et al. 2018).

For the characterization of the spatial structure of the obtained patterns, we use the global Kuramoto order parameter which is defined in a similar way as the local order parameter shown in Figure 5*D*, albeit it does not measure the synchrony only in a small local neighborhood, but involves averaging over the whole network. For a mathematical definition see Appendix C. The global order parameter r varies between 1 and 0, and $r = 1$ corresponds to the completely synchronized state in the system. Small values denote spatially desynchronized states.

Chimera states, which we observe for small values of the coupling strength σ both in networks with empirical structural connectivity, and networks with modular fractal connectivity, have a complex spatial structure due to the complexity of the network topologies and the absence of natural spatial ordering, in contrast to ring networks as studied in the previous section.

For the empirical network dynamics qualitatively similar to the dynamics of epileptic seizures can be computed. Spontaneous or driven high coherence events occur, indicating pathological seizure behavior. In Figure 8(*A*) an example of such a spontaneous event is given. The temporal evolution of the global order parameter $r(t)$ for a chimera state at fixed parameter values is shown. The temporal mean of the order parameter is $\langle r \rangle \approx 0{,}5$, and longer events of high coherence spontaneously occur. Before the high coherence event, a drop of the order parameter can be noticed, while the highest value of r is obtained right before its collapse. Both effects have been observed in the study of synchrony in epileptic seizures (Mormann et al. 2003, Jiruska et al. 2013), while a decrease of order preceding complete synchronization has been observed by Andrzejak et al. (2016) in a ring of nonlocally coupled phase oscillators. The high coherence events can be controlled by the coupling strength σ; strong coupling in the regime of chimera states increases their probability of occurrence. Furthermore, as shown in Figure 8(*B*), changing the coupling can induce switching between the chimera and the strongly synchronized state, which controls the pathological dynamics. It is interesting to note that the system needs some time to respond to modified coupling strength and the high synchronization event persists for some time, even after the coupling is changed back to its initial value. For more detailed computer simulations and comparison with recorded EEG data see Gerster et al. (2020).

5. Simulation of Unihemispheric Sleep

In this section we apply the FitzHugh-Nagumo model with the same empirical structural connectivity as in the previous section to study the phenomenon of unihemispheric sleep (Ramlow et al. 2019). We show that the dynamical asymmetry of the two brain hemispheres, induced by the natural structural asymmetry, can be enhanced by introducing the inter-hemispheric coupling strength as a control parameter for partial synchronization patterns. We discuss a minimum model elucidating the modalities of unihemispheric sleep in human brain, where one hemisphere sleeps while the other remains awake.

A well-known phenomenon in nature is unihemispheric slow-wave sleep, exhibited by aquatic mammals including whales, dolphins and seals, and multiple bird species.

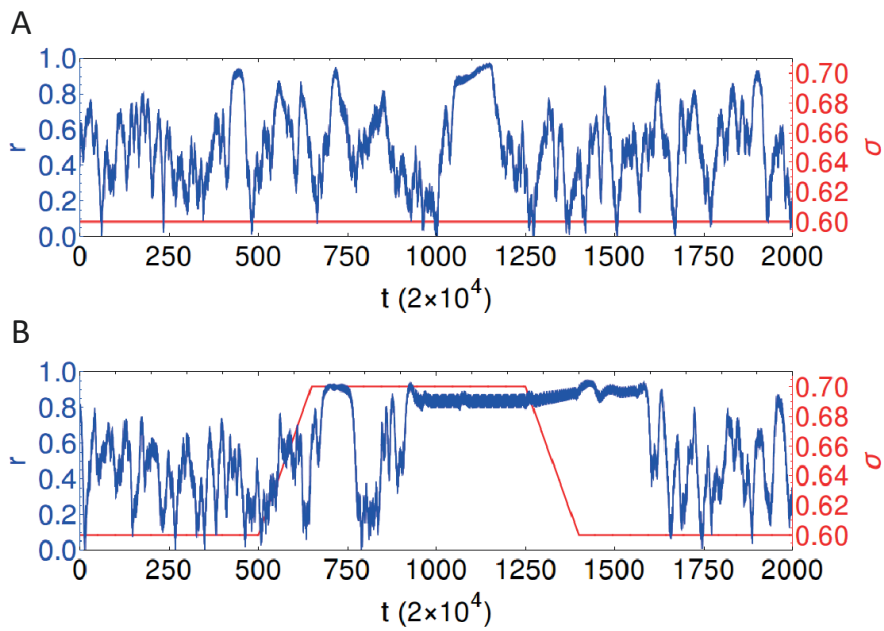

Fig. 8 Computer simulation of epileptic seizures with empirical structural connectivity: Temporal evolution of the global Kuramoto order parameter r shown in blue for the network with $a = 0.5$, $N = 90$. The coupling strength σ is shown in red. (*A*) Chimera state, constant coupling strength $\sigma = 0.6$; (*B*) controlled dynamics: coupling strength $\sigma = 0.6$ is increased to the value $\sigma = 0.7$ and kept fixed for the time interval $650 < t/2\times10^4 \leq 1350$, followed by decrease back to $\sigma = 0.6$, this causes the transitions between the chimera state and strongly synchronized states. (After Chouzouris et al. 2018.)

Unihemispheric sleep is the remarkable ability to engage in deep (slow-wave) sleep with a single hemisphere of the brain while the other hemisphere remains awake (Rattenborg et al. 2000, 2016, Mascetti 2016). Interestingly, sleep and wakefulness are characterized by a high and low degree of synchronization, respectively (Rattenborg et al. 2000). Sleep is associated with specific synchronized oscillations, i.e., sleep spindles and slow oscillations in the thalamocortical system (Steriade et al. 1993). In addition, arousal- and sleep-promoting neural assemblies undergo collective activity resulting in secretion of sleep-regulating neurotransmitters (Schwartz and Roth 2008). While the synchronization processes can differ

between adults and children (Spiess et al. 2018), transitions from wakefulness to sleep are widely accompanied by synchronization phenomena (Moroni et al. 2012).

In the human brain the first-night effect, which describes troubled sleep in a novel environment, has been related to asymmetric dynamics recently, i.e., a manifestation of one hemisphere of the brain being more vigilant than the other (Tamaki et al. 2016). Sleep is a dynamical macrostate of the brain that is observed over a wide range of animal species. Sleep is accompanied by a loss of consciousness and conscious perceptions, and muscle activity is reduced or absent. Sleep alternates between rapid-eyemovement (REM) and non-REM stages N1, N2, N3, where the latter are dominated by slow oscillations (1 Hz and below) which can also emerge locally (Vyazovskiy et al. 2011, Lesku et al. 2011). Sleep stage switching dynamics includes wake/sleep asymmetric stochasticity (Scammell et al. 2017), but obeys an underlying control by regulatory circuits forming bistable biological flipflop switches (Saper et al. 2001, Fuller et al. 2006, Saper et al. 2010, Brown et al. 2012), and sleep regulation is coupled to the sleep oscillations of the thalamocortical system (Schellenberger Costa

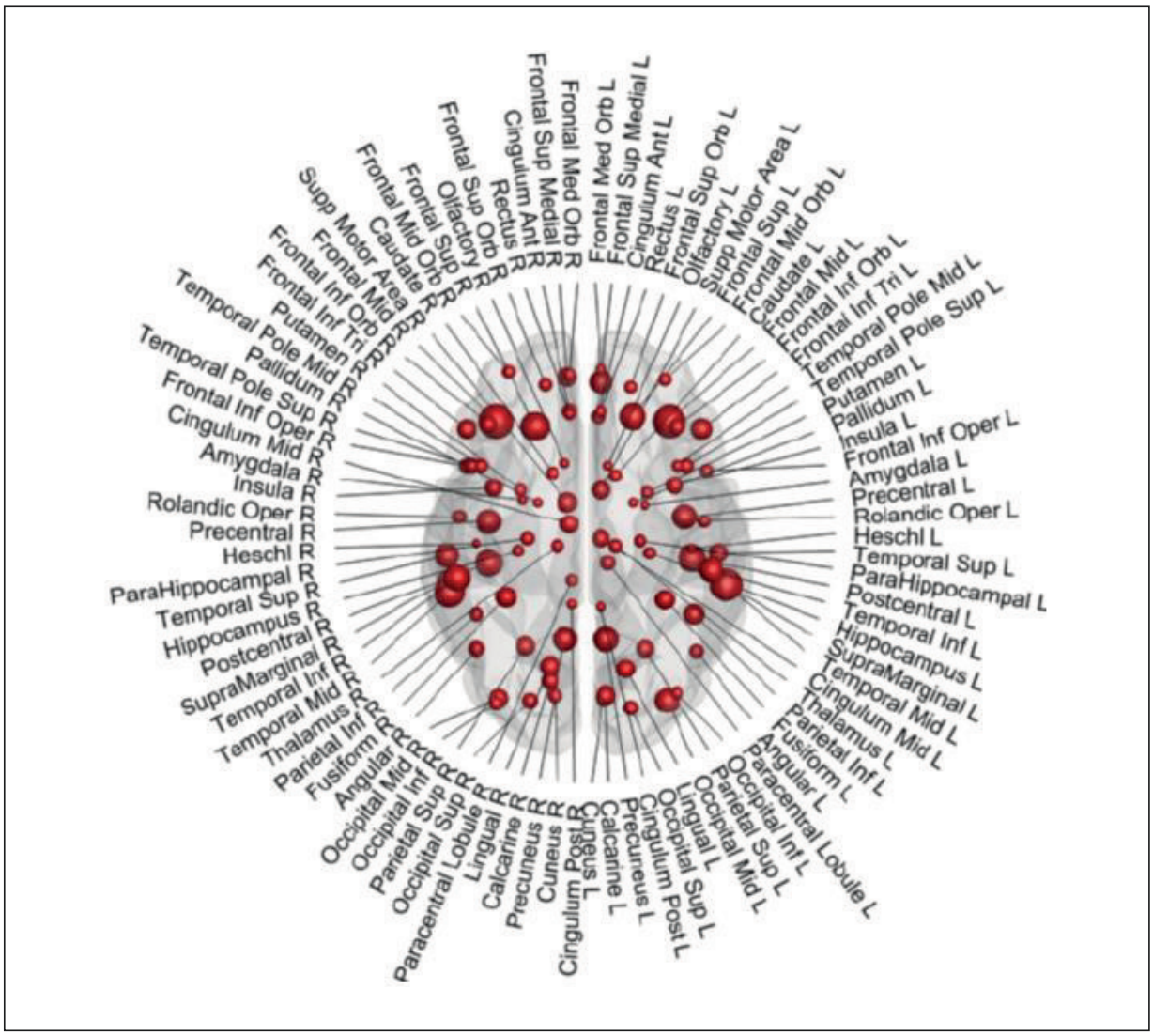

Fig. 9 Human brain regions from the Automated Anatomic Labeling (AAL) atlas (Tzourio-Mazoyer et al. 2002), which are used as nodes in the brain network incorporated in the following computer simulations.

et al. 2016). While most animals follow a similar qualitative sleep pattern and fall into sleep with both hemispheres, in certain bird and mammal species sleep can be unihemispheric (Mascetti 2016).

It has been speculated that unihemispheric sleep is related to the spontaneous symmetry-breaking phenomenon of chimera states in oscillator networks (Abrams et al. 2008, Motter 2010).

While the neurophysiological processes that ensure the existence of this dynamical state of unihemispheric sleep remain largely unknown, it is presumed that a certain degree of structural interhemispheric separation is a necessary condition for this pattern to persist. Therefore, we propose to model unihemispheric sleep by a two-community network of the two hemispheres where the inter-hemispheric coupling strength is smaller than the intra-hemispheric coupling. We model the spiking dynamics of the neurons by the paradigmatic FitzHugh-Nagumo model, and investigate possible partial synchronization patterns (Ramlow et al. 2019).

We consider the same empirical structural brain network as in the previous section (Chouzouris et al. 2018), shown in Figures 9 and 10, where every region of interest is modeled by a single FitzHugh-Nagumo oscillator.

The brain network was obtained from diffusion-weighted magnetic resonance imaging data measured in healthy human subjects (Melicher et al. 2015). The data were analyzed using probabilistic tractography as implemented in the FMRIB Software Library, where FMRIB stands for Functional Magnetic Resonance Imaging of the Brain. The anatomic network of the cortex and subcortex is measured using Diffusion Tensor Imaging and subsequently divided into 90 predefined regions according to the Automated Anatomical Labeling (AAL) atlas (Tzourio-Mazoyer et al. 2002). Each node of the network corresponds to a brain region. Indirect information of the white matter fibers connecting different brain regions is provided by diffusion-weighted Magnetic Resonance Imaging (dMRI) measuring the preferred diffu-

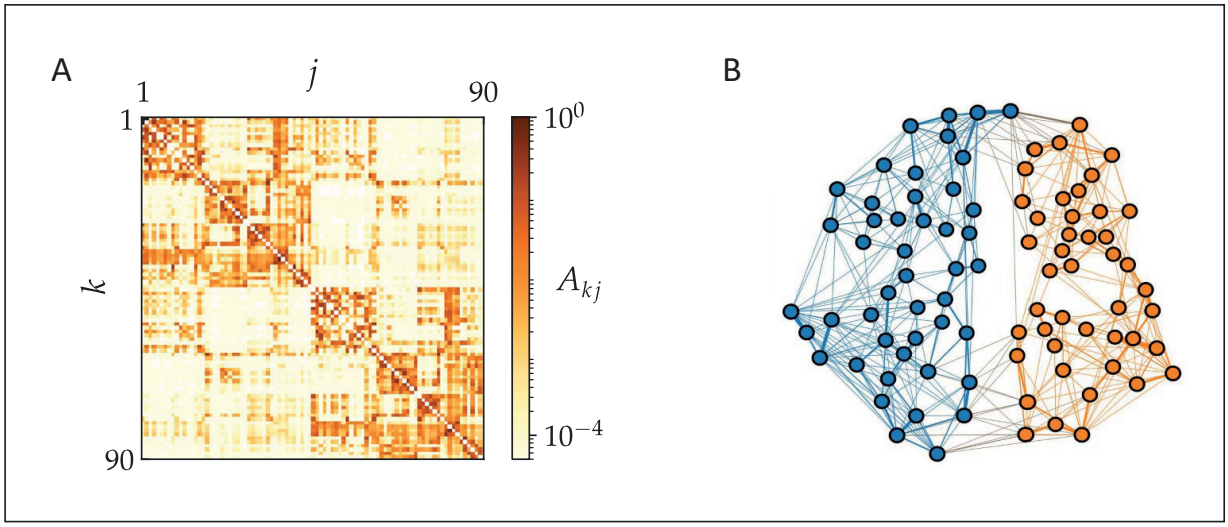

Fig. 10 Model for the hemispheric brain structure: (*A*) Weighted coupling matrix A_{kj} of the averaged empirical structural brain network derived from twenty healthy human subjects by averaging over the coupling between two brain regions k and j. The 90 brain regions k, j are taken from the Automated Anatomic Labeling atlas in Fig. 9, re-labeled such that $k = 1, ..., 45$ and $k = 46, ..., 90$ correspond to the left and right hemisphere, respectively. (*B*) Schematic representation of the graph of the brain structure with highlighted left (dark blue) and right (light orange) hemisphere. (After Ramlow et al. 2019.)

sion direction in each voxel of the brain. Probabilistic tractography then provides for each voxel a set of $n_s = 5000$ streamlines, simulating the possible white matter fiber tracts. A coefficient P_{kj} giving the connectivity probability from the k-th to the j-th region is introduced by the proportion of streamlines connecting voxels in region k to voxels of region j on the condition that they originate in region k. Thus a weighted adjacency matrix of size 90 × 90, with node indices $k \in N = \{1, 2, ..., 90\}$ is constructed. Finally, each entry in this adjacency matrix, i.e., the connectivity between every two regions, is averaged over 20 subjects (mean age 33 years, standard deviation 5.7 years, 10 females, 2 left-handed) yielding the average empirical structural brain network $\mathbf{A} = \{A_{kj}\}$. The pipeline for constructing the structural network has been adopted from previous study of differences in connectivity patterns between healthy subjects and schizophrenia patients (Cabral et al. 2013). Obtaining such connectivity information using diffusion tractography is known to face a range of challenges (Schilling et al. 2019, Hlinka and Coombes 2012). Note that there is a very slight structural asymmetry of the two brain hemispheres. This structural asymmetry is well described in the neuroscience literature and is related to the known asymmetries in localization of psychological functions, such as the prevalence of language functions in the left brain hemisphere in humans. Moreover, this lateralization is known to differ between genders as well as age. Note that while a weak but systematic asymmetry between the hemispheres (difference between the strength of corresponding connections in the left and right hemisphere, Wilcoxon rank sum test, $p < 0.01$) was observed in our data set in more than 20 % of the connections – most prominently in the temporal cortex – we did not observe significant variation of the asymmetry with gender, age, or handedness. This can probably be attributed to the relatively small size of our sample that provides information about the general structure and asymmetry of the brain, but not about its subject-specific variability.

The FitzHugh-Nagumo equations (see Appendix A) are now split into two sets for the right and left hemisphere, respectively, with $k \in N_{\mathrm{H}}$ where N_{H} denotes either the set of nodes k belonging to the left (N_L) or the right (N_R) hemisphere. The coupling within the hemispheres is given by the intra-hemispheric coupling strength σ, while the coupling between the hemispheres is given by the inter-hemispheric coupling strength ς. The synchronization is characterized by the hemispheric Kuramoto order parameter $R_H(t)$ which is defined in analogy to the global Kuramoto order parameter, however, the averaging is not over the whole network, but only over one hemisphere H, either the left ($H = L$) or right ($H = R$), see Appendix C.

To achieve partial synchronization patterns we consider the inter-hemispheric coupling strength ς as an independent parameter that allows us to reduce the coupling between the hemispheres. This is motivated by the presumption that sleeping with one hemisphere at a time requires a certain degree of hemispheric separation (Rattenborg et al. 2000). All other parameters remain unchanged. In a certain intermediate interval of inter-hemispheric coupling strength $\varsigma < \sigma$ we find the partial synchronization pattern shown in Figure 11 where the left hemisphere is incoherent while the right is frequency-synchronized, except for three small brain regions (hippocampus, gyrus parahippocampalis, and amygdala). This shows up in the space-time plot, in the mean phase velocity profile, and in the hemispheric Kuramoto order parameter (although there is no perfect phase synchronization resulting in $R_R < 1$). Note that the incoherent, left hemisphere occasionally exhibits a high degree of synchronization that, in contrast to the right hemisphere, is unstable and vanishes after a short while. In conclusion, we have investigated the dynamical asymmetry arising from the structural difference between the two brain hemispheres. We have varied the interhemispheric coupling strength, while

keeping the intra-hemispheric coupling strength fixed, to increase the degree of inter-hemispheric separation, ranging from isolated to fully coupled hemispheres. This has resulted in the observation of partial synchronization patterns similar to spontaneously synchrony-breaking chimera states. These partial synchronization patterns occur for coupling strengths where the isolated hemispheres are frequency-synchronized while the brain network with equal intra- and inter-hemispheric coupling remains completely incoherent. By tuning the coupling between the hemispheres, we have shown that at intermediate inter-hemispheric coupling one hemisphere becomes incoherent, giving rise to a chimera-like partial synchronization pattern.

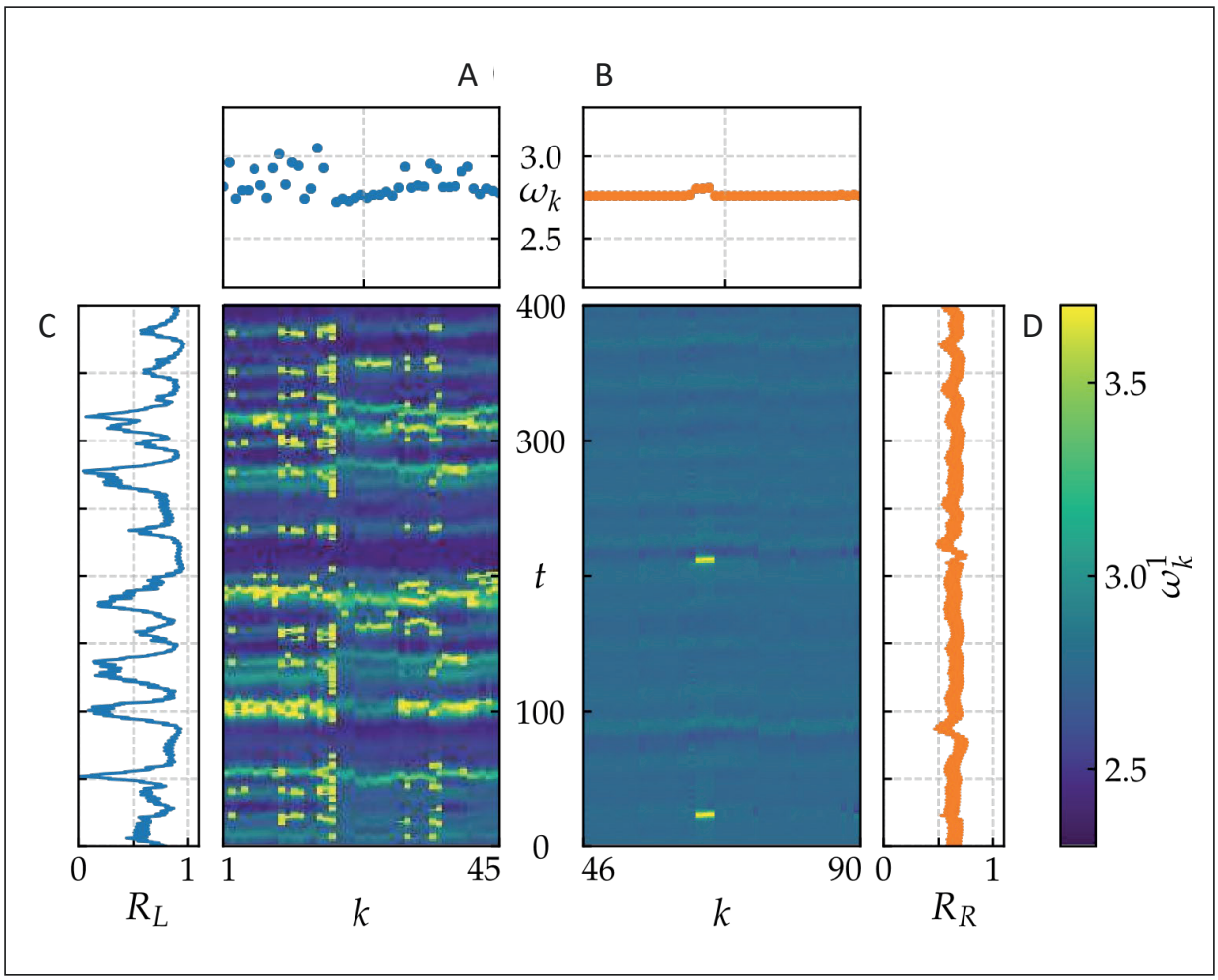

Fig. 11 (Color online) Partial synchronization pattern for $\sigma = 0.70$, $\varsigma = 0.15$ with low and high degree of synchronization in the left (*A*, *C*) and right (*B*, *D*) hemisphere, respectively. (*A*, *B*) Mean phase velocity profiles ω_k. (*C*, *D*) Inner panels: space-time plots of node-wise phase velocity ω_k^1 averaged over a single oscillation, outer panels: hemispheric Kuramoto order parameter $R_{L,R}$ as a function of time *t*. Other parameters as in Fig. 5. (After Ramlow et al. 2019.)

These results are in accordance with the assumption that unihemispheric sleep requires a certain degree of inter-hemispheric separation. Moreover, it is known that the brain is operating in a critical state at the edge of different dynamical regimes (Massobrio et al. 2015), exhibiting hysteresis and avalanche phenomena as seen in critical phenomena and phase transitions (Steyn-Ross and Steyn-Ross 2010, Ribeiro et al. 2010, Kim et al. 2018). By choosing appropriate coupling parameters, we have also found an intriguing dynamical behavior regarding the

transition from frequency to phase synchronization. We observe that in this regime our brain model exhibits spontaneous symmetry breaking and bistability, where each hemisphere may engage into either of two dynamical states, characterized by a relatively high and low degree of synchronization. However, a high degree of synchronization in one of the hemispheres always coincides with a low degree of synchronization in the other. To sum up, the structural asymmetry in the brain allows for partial synchronization dynamics, which may be used to model unihemispheric sleep or explain the mechanism of the first-night effect in human sleep.

6. Conclusions and Outlook

Chimera states are intriguing partial synchronization patterns occurring in a variety of networks in nature and technology. They combine spatially separated domains of synchronized and desynchronized rhythms and are connected with scenarios leading from complete synchronization to complete desynchronization. Here we have focussed on applications to neuroscience, and presented computer simulations of neural networks modelling the brain. Starting from simple regular ring topologies with nonlocal coupling, we have considered more complex network topologies, e.g., mathematically constructed networks with fractal connectivity generated by a hierarchical iterative algorithm, and empirical structural neural connectivities derived from diffusion-weighted magnetic resonance imaging of humans. This has allowed us to obtain deeper insight into the structure and functionality of the brain. In all of these network topologies, and with various different models of local dynamics, chimera patterns have been found in computer simulations. In this review, we have restricted ourselves to the simple paradigmatic FitzHugh-Nagumo model of excitable media to describe the dynamics of the individual network nodes.

Typically, chimera states can be observed for weak coupling strength, and further increasing the coupling strength drives the system towards the completely coherent synchronized state. The knowledge of the possible dynamical regimes and transitions between them can be applied to the study of brain diseases, where synchronized behavior is often pathological, and to find possible ways to avoid it. As a prominent example we have presented computer simulations of epileptic seizures where the increased coupling strength leads to pathological synchrony, initiated or terminated via chimera states.

Further, we have focussed on unihemispheric sleep, where one hemisphere of the brain sleeps while the other remains awake. Human brains exhibit a slight structural asymmetry of their two hemispheres. We have investigated the dynamical asymmetry arising from this natural structural difference in healthy human subjects, using a minimum model which elucidates the modalities of unihemispheric sleep in the human brain. In fact, this state is common among migratory birds and mammals like aquatic species like whales, dolphins, seals, but has only recently been associated with the “first-night effect” in human sleep, i.e., the observation of troubled sleep in a novel environment. The structural asymmetry in the brain allows for partial synchronization dynamics and spontaneous dynamic symmetry breaking of the two brain hemispheres in the form of a chimera, which may be used to model unihemispheric sleep or explain the mechanism of the first-night effect in human sleep, since different sleep stages are associated with different degrees of synchronization.

Future promising perspectives of the research on chimeras are, for instance, chimera patterns in small networks, adaptive networks, in two and three spatial dimensions, complex coupling

topologies like modular, fractal, or multilayer connectivity, coupled phase and amplitude dynamics, information flow in chimera states, as well as filtering and control methods for stabilizing chimera states (Schöll et al. 2020). Time delay, which is ubiquitous in real-world systems, has been identified as a powerful tool for control of general synchronization patterns: It allows for observation of novel synchronization scenarios where the coherent domains of chimera states in the outer layers of multiplex networks are synchronized, while the incoherent domains are not (Sawicki et al. 2018). The middle relay layer remains desynchronized and exhibits various multi-chimera patterns, or even chaotic dynamics. Furthermore, partial relay synchronization of chimeras states in the outer layers has been realized in the form of intriguing double chimeras, where the coherent domains in both layers are synchronized, while the incoherent ones are not. By choosing an appropriate value for the time delay one can switch between the different synchronization scenarios. Quantum signatures of chimera states like bosonic squeezing, weighted quantum correlations, and measures of mutual quantum information (Bastidas et al. 2015) also offer promising directions of future research.

Appendix A: The FitzHugh-Nagumo Model

In the Appendices we give the detailed mathematical expressions used for the computer simulations in the main text. The FHN model describes neural areas by two simple differential equations for an activator variable (the membrane potential) and an inhibitor variable (recovery variable). We consider a network of N nonlocally coupled FHN oscillators (Omelchenko et al. 2013, 2015a):

$$\varepsilon \frac{du_k}{dt} = u_k - \frac{u_k^3}{3} - v_k + \sigma \sum_{j=1}^{N} A_{kj}\left[b_{uu}\left(u_j - u_k\right) + b_{uv}\left(v_j - v_k\right)\right], \qquad [1a]$$

$$\frac{dv_k}{dt} = u_k + a + \sigma \sum_{j=1}^{N} A_{kj}\left[b_{uu}\left(u_j - u_k\right) + b_{uv}\left(v_j - v_k\right)\right], \qquad [1b]$$

where u_k and v_k, $k = 1, \ldots, N$ are the activator and inhibitor variables, respectively, A_{kj} is the coupling matrix of the network, $\varepsilon > 0$ is a small parameter characterizing a timescale separation between the fast activator and the slow inhibitor, and σ denotes the coupling strength. All indices are modulo N. Depending upon the threshold parameter a, each individual FHN unit exhibits either oscillatory ($|a| < 1$) or excitable ($|a| > 1$) behavior. Self-sustained oscillatory behavior means that the steady state is unstable, and a limit cycle, i.e., a periodic trajectory, is born, while excitable behavior means that the steady state is locally stable, but single spikes can be generated by supra-threshold excitation.

The important feature of Equations [1a, b] is that they contain not only direct u–u and v–v couplings, but also cross-couplings between activator (u) and inhibitor (v) variables, which we model by a rotational coupling matrix:

$$\mathbf{B} = \begin{pmatrix} b_{uu} & b_{uv} \\ b_{vu} & b_{vv} \end{pmatrix} = \begin{pmatrix} \cos\varphi & \sin\varphi \\ -\sin\varphi & \cos\varphi \end{pmatrix} \qquad [2]$$

Therefore, the matrix **B** is determined by the coupling phase φ.

We assume that all elements are in the oscillatory regime and identical, i.e., $-1 < a < 1$. For a one-dimensional ring topology of N nonlocally coupled FHN oscillators, where each element is coupled to R neighbors on either side (Omelchenko et al. 2013), the coupling term in Equations [1a, b] becomes

$$\sigma \sum_{j=1}^{N} A_{kj} = \frac{\sigma}{2R} \sum_{i=k-R}^{k+R} \qquad [3]$$

Appendix B: Local Order Parameter

The spatial coherence and incoherence of the chimera state can be characterized by a real-valued local order parameter (Wolfrum et al. 2011, Omelchenko et al. 2011]

$$Z_k = \left| \frac{1}{2\delta} \sum_{|j-k| \le \delta} e^{i\theta_j} \right|, \; k = 1, \ldots, N \qquad [4]$$

where $\theta_j = \arctan(v_j/u_j)$ denotes the geometric phase of the j-th FHN unit. We use a spatial average with a window size of $\delta = 25$ elements. A local order parameter $Z_k = 1$ indicates that the k-th unit belongs to the coherent part of the chimera state, and Z_k is less than 1 for incoherent parts.

Appendix C: Global Order Parameter

For the characterization of the spatial structure of the obtained patterns in Section 4 we use the global Kuramoto order parameter $r = \left| \frac{1}{N} \sum_{k=1}^{N} e^{i\phi_k} \right|, \; k = 1, \ldots, N$, where φ_k is the dynamical phase. In the uncoupled case, the geometrical phase is defined as $\theta_k = \arctan(v_k/u_k)$. The function $t(\theta_k)$ is calculated numerically, assigning a value of time $0 < t(\theta_k) < T$ for every value of the geometrical phase, where T is the oscillation period. The dynamical phase is then defined as $\phi_k = 2\pi \cdot t(\theta_k)/T$, which yields constant phase velocity $\dot{\phi}_k$. The global order parameter varies between 1 and 0, and $r = 1$ corresponds to the completely synchronized state in the system. Small values denote spatially desynchronized states.

The synchronization of the brain hemispheres in Section 5 is characterized by the hemispheric Kuramoto order parameter:

$$R_H(t) = \frac{1}{45} \left| \sum_{|k \in N_{\mathrm{H}}} \exp[i\phi_k(t)] \right|, \qquad [5]$$

where H denotes either the left ($H = L$) or right ($H = R$) hemisphere.

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