



Dynamic primitives of brain network interaction^a

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A B S T R A C T

What dynamic processes underly functional brain networks? Functional connectivity (FC) and functional connectivity dynamics (FCD) are used to represent the patterns and dynamics of functional brain networks. FC(D) is related to the synchrony of brain activity: when brain areas oscillate in a coordinated manner this yields a high correlation between their signal time series. To explain the processes underlying FC(D) we review how synchronized oscillations emerge from coupled neural populations in brain network models (BNMs). From detailed spiking networks to more abstract population models, there is strong support for the idea that the brain operates near critical instabilities that give rise to multistable or metastable dynamics that in turn lead to the intermittently synchronized slow oscillations underlying FCD. We explore further consequences from these fundamental mechanisms and how they fit with reality. We conclude by highlighting the need for integrative brain models that connect separate mechanisms across levels of description and spatiotemporal scales and link them with cognitive function.

1. Introduction

Neural activity oscillates: neurons and neural populations transiently entrain in synchronized movements, rhythmically coupling and uncoupling (Buzsaki, 2006). This intermittent synchronization between neuron populations is mediated by the underlying structural network of axon bundles and can span over widespread areas of the brain, engaging neural populations to form functional networks that are active during task and rest (Smith et al., 2009). Functional networks were found in slow (<0.1 Hz) functional magnetic resonance imaging (fMRI) activity, but similar network patterns were also found with faster magnetoencephalography (MEG) and electroencephalography (EEG) (Brookes et al., 2011; Hipp et al., 2012). A compact way to represent functional networks are FC matrices where each entry quantifies the correlation or other statistical measures of association between every pair of brain signals in a data set (Bullmore and Sporns, 2009). The longer

the time series used to compute FC (several minutes to hours) the more static and conserved is the network pattern. Computed over short time windows (seconds to minutes), the FC pattern changes rapidly, which is called dynamic FC (dFC) or short-term FC (Lurie et al., 2020; Preti et al., 2017). To characterize the evolution of dFC the window is slid over a longer time series and the dFC matrices at different times are compared with each other, e.g., by pairwise correlation. The results are then written into another matrix, called FCD matrix (Hansen et al., 2015), where each axis encodes the time points of the time series (see Fig. 2 for exemplary static FC and FCD). For example, the matrix entry at row 20 and column 30 would contain the correlation coefficient between the dFC matrix computed at time point 20 and the dFC matrix computed at time point 30. FCD matrices often show a checkerboard pattern with quadratic blocks, indicating that dFC configurations form, exist for a while, dissolve and re-occur at a later point in time (Hutchison et al., 2013), which is interpreted to reflect an ongoing transitioning between

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brain states (Kringelbach and Deco, 2020), like the transition from sleep to wakefulness (Deco et al., 2019). While FC can be computed with a variety of different methods, the essential aspect we are focusing on is the synchrony or coherence between time series, that is, the tendency of recurrent activity patterns (waves, oscillations) to engage in constant relative phase relationships; therefore, the conclusions drawn from the reviewed papers are relatively independent from a specific FC method as the commonly used methods like correlation, mutual information, or phase synchrony indices are all able to express aspects of synchrony (Bakhshayesh et al., 2019; Bastos and Schoffelen, 2016). Research on empirical data is paralleled by theoretical brain network modelling studies that help to relate FC(D) to the dynamics of networks of neuron population models (Breakspear, 2017). The key idea of brain network modelling is to study the dynamics that emerge when we couple models of local neural activity (Deco et al., 2008) according to 'structural connectivity' (SC), which is an aggregated description of the large-scale neuroanatomic fibers network that quantifies coupling strengths and time delays between brain areas (Calamante, 2019; Yeh et al., 2021). That is, the brain is considered as a graph where nodes represent brain areas connected by edges that represent axons, fiber bundles, or electrical synapses, which is then formalized as a dynamical system of coupled differential equations (Breakspear, 2017; Sanz-Leon et al., 2015). Simulated node time series are then related to empirical recordings like local field potentials, membrane potentials, firing rates, or synaptic activities to study the performance of the model (Ritter et al., 2013). Furthermore, the simulated activity is used to predict the signals of noninvasive techniques like fMRI, EEG or MEG using so-called forward models. For example, to predict blood-oxygen-level-dependent imaging (BOLD) fMRI signals the simulated time series are convolved with a hemodynamic response function or input to a Balloon-Windkessel hemodynamic model, which describe the transduction of neural activity into perfusion changes and the coupling of the latter with the BOLD signal (Friston et al., 2003; Sanz-Leon et al., 2015). After simulation, the predicted region-wise fMRI time series can be used to compute simulated FC and FCD matrices and compare them with their empirical counterparts in order to fit the parameters and to validate or falsify the model.

SC is usually estimated using diffusion-weighted MRI (dwMRI) tractography in humans (Sotiropoulos and Zalesky, 2019) and tract tracing in mouse (Oh et al., 2014) and monkey (Markov et al., 2013; Stephan et al., 2001). DwMRI tractography is a noninvasive technique for the virtual reconstruction of the pathways of white-matter fiber tracts that are then aggregated for each pair of brain regions to build comprehensive maps of large-scale white-matter connectivity. Tractography is controversial as it is known to be prone to errors like over-weighting simple and straight pathways and underweighting complex fiber configurations (Calamante, 2019; Jeurissen et al., 2019; Sampaio-Baptista and Johansen-Berg, 2017). One major limitation of dwMRI tractography is that we cannot directly measure all the relevant microstructural properties that influence coupling weights or transmission velocities of fiber tracts (Sotiropoulos and Zalesky, 2019). That is, even if the density or number of fibers could be reliably estimated, as attempted with dwMRI tractography, axonal connection strengths depend on more than just the number of axons, e.g., the number of synapses, axon diameter, spines and myelination, which implicates that tractography results must be interpreted with caution (Jeurissen et al., 2019; Yeh et al., 2021). Reconstructing fiber pathways is based on a mapping from water diffusion to fiber orientations, which is in general an ill-posed problem as MRI voxels are too large to resolve axons; neither the orientation of axon bundles in a voxel can be resolved, nor can different arrangements like bending, fanning, crossing or kissing be distinguished (Sotiropoulos and Zalesky, 2019). Consequently, tractography does not provide a direct measure of connection weights or time delays, but only a model-based estimation of streamline counts and their lengths, which are then used to approximate interregional coupling strengths and time delays. To mitigate this problem there are efforts to combine the results from tractography and invasive tract-tracer studies in mouse and mon-

key, which, for example, allows to constrain the directionality of fibers reconstructed with tractography (Shen et al., 2019).

As SC can be assumed to remain relatively static, a central question of BNM research is: how does the diverse repertoire of dFC configurations emerge from a fixed white matter connectivity? While many different local population models have been found to have comparable qualities for simulating static FC patterns, only a subset of those were able to simulate realistic dFC and FCD (Cabral et al., 2017). Depending on the underlying modeling assumptions, population model dynamics differ considerably with respect to their complexity and biophysical realism, ranging from detailed spiking neuron models, over neural field or neural mass models that simulate average features of neural populations, to highly abstract models with no clear interpretation in terms of physiological entities (Deco et al., 2008; Sanz-Leon et al., 2015). In large-scale BNMs the nodes are usually entire brain areas that contain millions of neurons and are therefore not simulated by spiking neurons, but rather by simplified models that simulate the combined behavior of a population of neurons, like the ongoing fluctuation of the mean population firing rate or of the mean membrane potential at each node. Together the state variables of all nodes span a high-dimensional phase space where each point corresponds to a unique combination of the system's states. In the phase space the system's equations prescribe a flow that defines how the system evolves when it starts at a given point. That is, phase flow links into trajectories, called orbits, that form geometric structures in phase space that capture the relevant characteristics of the system's dynamics (Izhikevich, 2007). For example, so-called fixed-point attractors correspond to a steady state solution of the system, while a limit cycle corresponds to periodic activity, like the regular spiking of a neuron or the oscillation of a brain rhythm. Even simple deterministic systems can show complex phase space geometries with so-called strange attractors characterized by unstable, diverging orbits, leading to chaos, with apparently random (but fully deterministic) behavior and strong sensitivity to initial conditions (Izhikevich, 2007). Studying the behavior of models in phase space in such a manner gives researchers the opportunity to explain specific observations from empirical data and dedicated models in terms of generic properties of dynamical systems, as we review below. In this context it is important to note that the number of existing studies that use systems of differential equations to analyze the mechanistic origin and emergence of FC(D) is rather limited and in some cases there exists just a single study that models a particular mechanism, which limits the degree to which this review can distinguish general results from results that are specific to a given model implementation.

In this article we review research that links the emergence of FC(D) to the ongoing fluctuation of synchronization and desynchronization of population activity, focusing on building an intuitive understanding of dynamical systems concepts and providing references to primary literature for more details. A fundamental set of related observations from empirical data and computational modelling is that functional networks, firing rates, BOLD amplitudes, and the power and phase of EEG/MEG bands collectively increase and decrease in a manner that is coordinated with the increase and decrease of the coherence between neural activity time series, a process that we call 'intermittent synchronization', which results in an ongoing fluctuation of the sliding window correlation between neural time series and hence the observed FCD (Allen et al., 2014; Betzel et al., 2016; Breakspear et al., 2004; Cabral et al., 2014; Esfahlani et al., 2020; Freyer et al., 2011, 2009; Honey et al., 2007; Magri et al., 2012; Schirner et al., 2018; Zalesky et al., 2014). This ongoing fluctuation of synchrony is important for behavior as it predicts the performance of perception, decision-making, attention, expectancy and predictive processing (Engel et al., 2001; Freyer et al., 2013; Haegens et al., 2021, 2012). Importantly, invasive recordings show a direct link between neural synchrony, firing and behavioral performance as the power of the alpha rhythm predicts task performance and firing rates in monkey discrimination tasks (Haegens et al., 2011). Likewise, brain disorders such as schizophrenia, epilepsy, autism, Alzheimer's, and Parkinson's disease were associ-

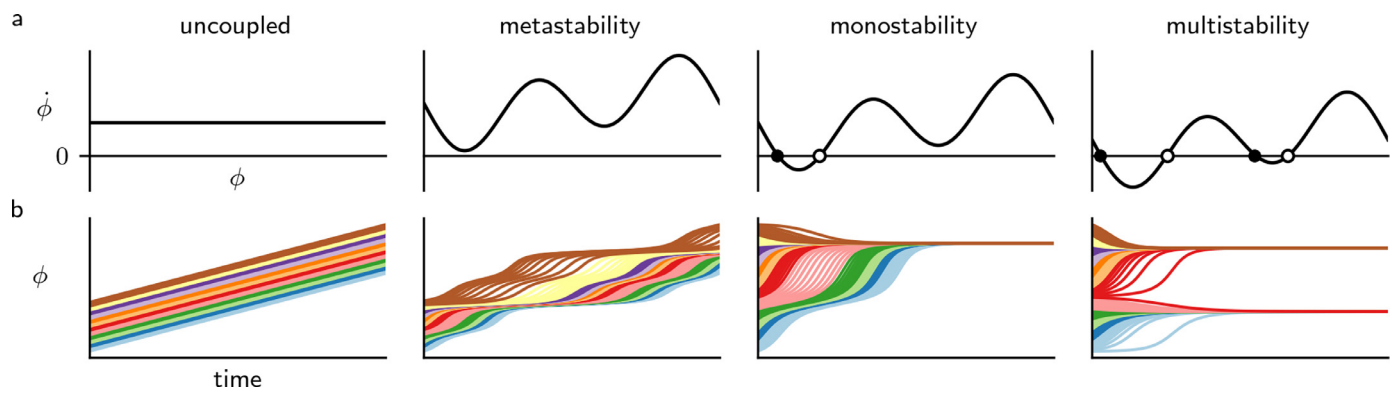


Fig. 1. Illustrating how a system switches between multistability and metastability as a control parameter changes. a, Trajectories of the extended HKB model (Haken et al., 1985) that relate the relative phase ϕ between two coupled oscillators to its change in time $\dot{\phi}$. In mono- and multistable systems the state converges onto an attractor (e.g., a point, which corresponds to a steady state solution or a limit cycle, which corresponds to periodic oscillations) after initial transients. An attractor is stable if all solutions starting sufficiently near will ultimately approach it, while in the case of an unstable attractor all nearby solutions diverge from it. Metastable systems are stable only on short timescales and spend a long time in states that change extremely slowly, but that are far from stable or unstable solutions. Stable fixed-point attractors are represented with filled circles and unstable fixed points with unfilled circles. b, Exemplary time series corresponding to the four different dynamical regimes in each column for different initial conditions. In the multistable regime (fourth column) the system has two stable fixed points to settle in. Which one is observed depends on the initial conditions and the sizes of the basins of attraction. As the control parameter changes, the less stable fixed point disappears, but the stronger attractor and its repelling partner remain, rendering the system monostable (third column). For a further change of the control parameter the flow no longer intersects the x-axis: all the fixed points have disappeared, making the system metastable (second column). In the uncoupled regime (first column) the two oscillators behave independently. A key aspect of the metastable regime is that remnants of attraction and slow flow remain where fixed points used to be (ghost states) as can be seen in the corresponding time series, where the system intermittently dwells near the former fixed points. Successive visits to these remnants of the fixed points are intrinsic to the system and do not require any additional sources of input.

ated with abnormal neural synchronization (Schnitzler and Gross, 2005; Uhlhaas and Singer, 2006).

While synchronization can be simulated with models of coupled oscillators, the mathematical analysis and theoretical understanding of synchronization is a hard problem (Mirollo and Strogatz, 1990). The good news is that to understand their behavior we do not have to seek out specific mechanisms for different physical, chemical, biological, or cognitive entities of interest, but it is sufficient to look at the generic behavior of dynamical systems, which is based on the same dynamic primitives (patterns of behavior that robustly emerge from different kinds of dynamic systems) regardless of spatial scale, form of implementation, functional interpretation or timescale (Kelso, 2012, 1995). Consequently, in the following we review how the emergence of slow correlated fluctuations underlying FC(D) can be explained by the dynamic mechanisms of multistability and metastability, irrespective of the specific type of neural model. Multistability refers to the coexistence of multiple stable system states, while in a metastable regime there exist no stable states and the system moves along sequences of states that are only intermittently stable on short time scales (Fig. 1, Table 1). These two basic mechanisms of dynamic systems behavior are closely related to the notions of 'stability'—in the brain, the ability of neural populations to sustain a state through reverberating activity—and 'criticality', which refers to ongoing dynamic instability reflected by scale-free spatial and temporal pattern formation (Bak et al., 1987). 'Scale-free' here indicates that the probability distribution of system variables does not have a characteristic time or length scale, but rather follows a power-law distribution. Criticality is highly relevant for brain sciences as the associated scale invariance is getting increasingly apparent in the brain (Beggs and Timme, 2012; Chialvo, 2010) and function can be closely linked across multiscale processes, ranging from molecular to system levels (Muñoz, 2018). Power-law scaling can be observed, for example, in fMRI (He, 2011), EEG (Linkenkaer-Hansen et al., 2001; Stam and De Bruin, 2004), electrocorticography (Miller et al., 2009), and slice preparations (Beggs and Plenz, 2003). Indeed, a central result from BNM research is that a BNM must be tuned close to the critical point of a bifurcation for the emergence of plausible multistable or metastable dynamics and FC(D) (Cabral et al., 2017; Deco and Jirsa, 2012). In addition, computational models suggest a range of adaptive benefits of

criticality including maximum dynamic range, optimal information capacity, storage, transmission and selective enhancement of weak inputs (Cocchi et al., 2017).

2. Attractors, bifurcations and multistable switching

The behavior of spiking and brain networks can be modelled by 'multistable attractor dynamics' (Amit and Brunel, 1997; Deco et al., 2008; Deco and Jirsa, 2012), which relates to the stability of the solutions of the underlying dynamical system under small perturbations of initial conditions (Izhikevich, 2007; Fig. 1). A stable attractor is an object in phase space that will ultimately be approached by all solutions that start sufficiently close, in the attractor's 'basin of attraction'; the term 'multistable' characterizes systems that have two or more coexisting attractors (Izhikevich, 2007). In contrast, if trajectories diverge away from them, solutions of dynamical systems are called 'unstable', or sometimes 'repellers'. Attractors can assume different shapes and configurations in phase space. For example, many neurons and neuron models exhibit a bistability where they switch between a resting (fixed-point) and a spiking (limit cycle) attractor. With fixed-point attractors the system tends to move towards and then settle in stationary 'equilibrium' states, like a constant firing rate or the quiescent state. On the other hand, limit cycle attractors correspond to closed trajectories in phase space and can therefore be used to describe oscillatory dynamics, like the tonic spiking of a neuron or the collective rhythm of a population (Deco et al., 2008). Importantly, when fixed-point or limit cycle units are (weakly) coupled they may synchronize themselves at a common rhythm with emerging slow coherent fluctuations of activity (Strogatz, 2000), which is fundamental for the emergence of correlated activity at different locations, that is, FC(D) (Cabral et al., 2017).

Critically, the study of dynamical systems reveals generic properties of complex systems that are conducive for intermittent synchronization and how these can be related with properties of biological neural networks (Strogatz, 2000). Tuning parameters like noise, external inputs, coupling, and others can cause transitions between attractors, destabilize existing attractors, or create new attractors. For example, without input a neuron is (typically) in a quiescent state, modelled by a fixed-point attractor. When a current is injected into the model (that is, a pa-

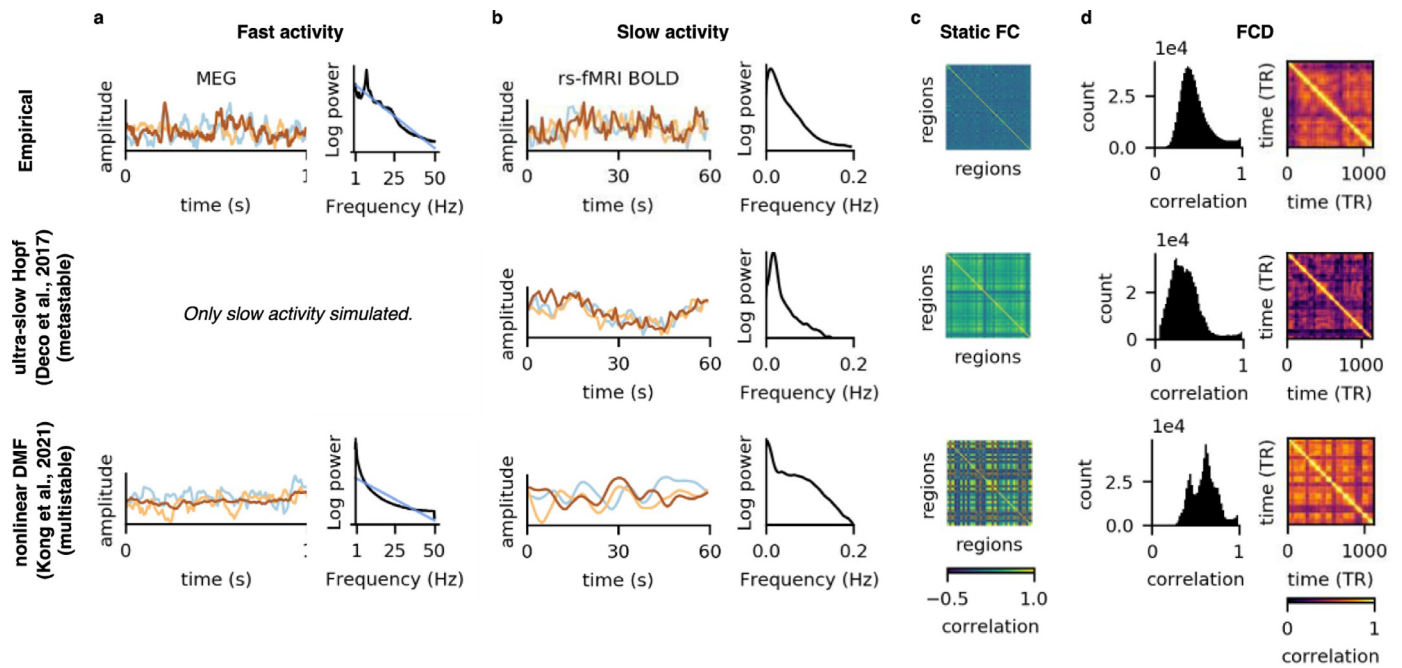


Fig. 2. Comparing empirical resting-state activity with simulated metastable (Deco et al., 2017b) and multistable dynamics (Kong et al., 2021). a, Exemplary time series of fast activity in three brain regions and averaged power spectra over all regions. MEG recordings show typical features of electromagnetic resting-state activity ($1/f$ relationship between power and frequency with a peak in the alpha range; blue line: line of best linear fit); the slow supercritical Hopf model is only simulated on the slow time scale; simulated synaptic activity time courses exemplify the dynamics of the nonlinear dynamic mean field model, which do not reproduce the $1/f$ shape and peak in the alpha range. b, Exemplary time series of slow activity in three brain regions and averaged power spectra over all regions. Resting-state fMRI is characterized by a peak in the slow range (0.001 - 0.1 Hz), which can be simulated by the supercritical Hopf model by directly setting the intrinsic frequency of Hopf oscillators; in the nDMF model slow synchronized oscillations become prominent when the fast simulated dynamics are forwarded to a hemodynamic model, which acts like a lowpass filter. c, static FC matrices computed over ~ 15 minutes of activity. d, FCD histograms and FCD matrices for dFCs with a window size of 60 seconds.

parameter is changed), and ramped up, it starts to fire tonic spikes, which corresponds to a limit cycle in phase space. Such qualitative transformations of the phase portrait in dependence of a parameter change are called 'bifurcations' (Fig. 1) and in our example the parameter 'input current' controls a bifurcation that separates the dynamics of a single stable equilibrium from a regime where several attractors coexist. Depending on the way in which the bifurcation changes the phase portrait it is called *supercritical* if stable objects appear when the system was tuned past the bifurcation point, for example, if stable limit cycle oscillations occur when the value of the control parameter is greater than a certain value; conversely, a bifurcation is *subcritical* when unstable objects appear, which allows for a regime of multistability where multiple stable objects (for example one fixed-point and one limit cycle separated by one unstable repeller) can co-exist (Izhikevich, 2007). Outside of the subcritical regime there is an either-or, but no co-existence of fixed-points and limit cycles. While the vicinity of a supercritical bifurcation is characterized by the emergence of slow, "critical", scale-free fluctuations, the dynamics in the vicinity of a subcritical bifurcation are governed by multistable switching (Freyer et al., 2012). This multistable switching is triggered by noise or regular inputs that move the state of the system over the boundaries of the respective basins of attraction. Such a noise-driven switching can also lead to slow oscillatory dynamics, but with strictly different statistics: while critical fluctuations follow a power-law, noise-driven multistable switching does not show scale-free properties. Rather, with large additive noise the transitions appear akin to a Poisson process and therefore follow an exponential distribution; small, state-dependent noise, on the other hand, leads to long dwelling in each state that follow a heavy-tailed exponential distribution (Freyer et al., 2012, 2011). Although characterized as multistable in the past, it is in some modelling studies often not fully clear to which degree slow synchronous oscillations are actually due to switching between the basins of attraction of different fixed-points (Deco and

Jirsa, 2012) or whether they emerge from a noise-driven exploration of the vicinity of a single fixed-point (Ghosh et al., 2008). Closer analysis and numerical exploration should be performed in future studies to better assess phase space behavior.

3. Multistability and slowing in bottom-up models

We now focus on the question how multistable units with fixed-point dynamics synchronize to explain the emergence of the correlated slow activity that makes up FC(D). Starting from a fixed-point solution and without any inputs the network would stay in its equilibrium state forever. This is different in stochastic simulations, where noise drives the system out of its fixed point(s) leading to an "exploration" of the respective basin of attraction (Pisarchik and Feudel, 2014). Ongoing noise can trigger a sequence of multistable switching from the basin of attraction of one attractor to another one with lifetimes of the different states that are on a considerably slower temporal scale compared to the intrinsic time scale of the model and the noise it receives (Arecchi et al., 1985). In addition to noise, another important precondition for the emergence of slow correlated fluctuations is the specific setting of parameters such that the system is close to a bifurcation where existing attractors become unstable and before new attractors stabilized, which leads to a critical slowing of the phase flow. Critical slowing refers to the tendency of a system to take longer to return to its attractor after perturbations and it has been observed in a diverse set of systems that underwent abrupt and rapid qualitative changes from ecosystems to medicine and finance (Kuehn, 2011). Importantly, critical slowing is accompanied by an increase in signal variance and autocorrelation and can be used as marker for the onset and termination of epileptic seizures (Maturana et al., 2020), the onset and termination of depression (van de Leemput et al., 2014), the onset of spiking in neurons (Meisel et al., 2015), or crashes in financial markets (May et al., 2008). Importantly, in BNMs the best fits

Table 1

Comparison of multistable and metastable dynamics and their functional consequences for explaining FC(D) with BNMs.

	(Multi)stability	Metastability
Description	existence of stable states (e.g., fixed-point and limit cycle attractors), mediated by (reverberating) input	states change extremely slowly, but are far from a stable or unstable state; states with long dwell times and slow evolution are connected by fast transients
Functional consequences	emerges in a subcritical regime near bifurcation where fixed point loses stability noise (or stimulation) drives exploration of basin of attraction and multistable switching between stable attractors dwell times follow exponential or stretched exponential distribution, depending on noise amplitude emergence of slow synchronized oscillations results from multistable switching and noise-driven exploration of basin(s) of attraction critical slowing as the system approaches a phase transition	emerges near supercritical Hopf bifurcation in between stable regimes system moves along sequences of metastable states ("heteroclinic orbits"); transitions not actively induced: neither noise nor parameter change required dwell times show a characteristic timescale, depending on noise amplitude emergence of slow synchronized oscillations results from fluctuating transient entrainment of limit cycle oscillations slow decay of metastable states with characteristic dwell-time distribution
Relation to FC	ghost states provide escapable regime with slow flow; small reconfigurations can turn ghost states into genuine attractors to stabilize function; makes repertoire of brain states available for rapid activation good quantitative capturing of spiking network attractors with mean-field models waveform shows transitions between noisy fixed point and limit cycle oscillations (e.g., waxing-and-waning of alpha rhythm) or between multiple fixed-points (e.g., quiescent and burst state) linearized models sufficient to explain FC pattern; analytic relationship between SC and static FC in linearized models best fit near edge of bifurcation where low-firing attractor becomes unstable best fit, highest variability and autocorrelation for intermediary coupling strengths	flexible switching between differently coordinated states; synchronization behavior is less constrained, large number of synchronization states with complex multiscale temporal structure a single parameter controls transition from stable to metastable dynamics in supercritical Hopf model waveforms express a combination of both noisy fixed-point dynamics and limit cycle oscillations; fast oscillators temporarily synchronize at slower delay-dependent network frequencies slow variations in the statistics of intermittent synchronization explains predicted FC pattern and slow oscillations in BOLD signal good fit over wide range of global coupling strengths and Hopf bifurcation parameters highest complexity, and variability for weak coupling strengths
Relation to FCD	increasing the number of attractors and noise (compared to FC models) necessary to instantiate dFC switching emergence of new network attractors required bistability in uncoupled units best fit for coupling strength that yields largest number of attractors, at a different point as in the case of static FC (where low-firing attractor loses stability)	slow fluctuation of dFC patterns results from the ongoing fluctuation of synchrony of transient couplings on faster time scales highest (closest to empirical) metastability is only present in narrow range of bifurcation parameter near supercritical Hopf bifurcation best fit very close to supercritical Hopf bifurcation where variability of brain phase synchrony configurations is maximized
Criticism (individually)	system can get "trapped" in stable states either noisy fixed-point dynamics or limit cycle oscillations, but not the complex waveform of fMRI time series or MEG envelope time series best fit with static FC, respectively FCD, is at different working points simplifying assumption in mean field analysis: only accounting for stationary states in studies often not fully clear whether dynamics characterized as "multistable" are actually switching between different basins of attraction or noise-driven exploration of the vicinity of a single (monostable) fixed-point attractor stationary equilibria and resulting "invariant" behavior at odds with variability and creativity of human behavior	system never settles for a time much longer or shorter than characteristic time scale mixture of noisy fixed-point dynamics and limit cycle oscillations, but only for single oscillation frequency very narrow range for optimal working point for FCD Hopf model is abstract, no direct relationship to physiological entities
Criticism (both)	spiking networks used to simulate brain areas are orders of magnitude smaller than in reality generic spiking network architectures do not account for the complex function and dynamics that may be embedded in microcircuit schemas structural connectivity (coupling strengths and time delays) is estimated from dwMRI data, no direct measurement simplifying assumptions in mean field analyses, e.g., only modelled around stationary states implausible frequency spectra no function (task-related activity) in BNM, only resting-state fixed parameters (e.g., no plasticity) no somatic afferents (brain without a body)	ongoing metastability at odds with fixation of function, e.g., through attentional mechanisms

between simulated and empirical FC have been found near the edge of a bifurcation where the low-firing attractor became unstable and before high-activity attractors stabilized, which led to the necessary slowing of the system (Deco et al., 2013; Deco and Jirsa, 2012).

Studying brain network activity from the bottom up, Deco and Jirsa (2012) simulated a detailed brain model, based on the spiking neuron networks from Brunel and Wang (2001), where populations of excitatory and inhibitory integrate-and-fire neurons were coupled using SC from dwMRI tractography, which yielded a global fixed-point attractor network. Under this model and parameterization the sum of all (external plus recurrent) inputs is slightly subthreshold, and firing is therefore primarily triggered by fluctuations of the input around the firing threshold, which drives the neurons to a state of "spontaneous" firing with excitatory cells firing asynchronously at a rate of 3 Hz and

inhibitory neurons at 9 Hz, which corresponds to typical values for spontaneous activity in the cerebral cortex (Burns and Webb, 1976; Koch and Fuster, 1989; Wilson et al., 1994). When the strength of (global) coupling between brain areas is increased, this low-firing ("spontaneous") attractor becomes unstable and high-activity attractors emerge where persistent fast firing is generated through recurrent excitation. Under this model the stabilization of the high-activity attractor is primarily mediated by recurrent activation in the global network.

Importantly, the emergence of slow (<0.1 Hz) synchronous oscillations and the best match between empirical and simulated FC occurred both near a critical value of global network coupling. When the mean inter-areal coupling strength was tuned towards such a critical point at the edge of a bifurcation, the spontaneous low-firing state became unstable and high-firing attractors emerged in the network. This region of

decreased stability was in the middle between two stable regions: for zero and very low values of global coupling only the trivial low firing attractor existed: this equilibrium state was stable and small random inputs had only a minor impact on the system's state. Likewise, for a very high value of global coupling the system was also stable and only a single (limit cycle) attractor existed: continuous firing, like in an epileptic seizure. Here, again, small random inputs had no big effect on the amplitude of oscillations. Also, in both extreme cases the simulated FC did not correspond well to empirical FC patterns. However, for intermediary values of global coupling a high correspondence with empirical FC and at the same time the highest variability (entropy) of simulated activity emerged, characterized by the co-existence of multiple attractors that corresponded to different configurations of high firing activity in particular brain areas, and which enabled the emergence of slow, oscillatory transitions between these attractors. Put into the language of graph theory, in the subcritical region at a low value of global coupling brain regions are effectively uncoupled—segregated—showing a lack of integration. Conversely, when global coupling is too high cortical activity is coupled too tightly and again only a trivial (e.g., hypersynchronous) state emerges, characterized by too much integration. However, near the critical point of a phase transition the system shows a dynamic balance between integration and segregation and an increased ability for spontaneous reconfiguration.

Slow synchronous fluctuations emerge close to a bifurcation when fixed-point attractors lose stability, which leads to a loss of attraction around the destabilizing fixed point, which in turn leads to a slowing of the time scale and long transients (Hastings et al., 2018). Such critical slowing is characteristic of many complex systems close to a critical point, where the time scale of fluctuations changes from a fast exponential to a slower power law process. It should be mentioned that such slowing does not imply that the entirety of system dynamics becomes slow, but only that unstable modes decay more slowly. With linear stability analysis, dynamic instability and slowing can be expressed by the Lyapunov exponent, which quantifies the rate of decay of small perturbations based on a local linear approximation (Kuehn, 2011). Far from the bifurcation the spontaneous state is strongly attractive, with exponential decay; when the associated, negative Lyapunov exponent approaches zero, the system approaches a phase transition and these fluctuations decay more slowly. However, at some point near the instability the local linearization breaks down and higher-order nonlinear effects increasingly contribute in a way that fluctuations no longer decay exponentially but can persist for longer, which increases autocorrelation and allows the emergence of correlated activity over larger distances and longer timescales (Kuehn, 2011). Slowing is also reflected in power spectral densities, where the power of low frequencies (<0.1 Hz) increases when global coupling increases (Deco et al., 2013). Furthermore, slowing near a critical point corresponds to sharp increases in the variation of the activity and its autocorrelation, leading to functional benefits (Shew and Plenz, 2013) like optimized information transmission (Beggs and Plenz, 2003), information storage (Haldeman and Beggs, 2005), computational power (Bertschinger and Natschläger, 2004), and dynamic range, the sensitivity to react to input across a broad spectrum of intensities (Kinouchi and Copelli, 2006).

Why do slow synchronized oscillations emerge at a critical working point? If the system would be instead in a stable subcritical state, then random microscopic fluctuations would remain confined to the microscopic scale, because the strong stable fixed-point damps fluctuations on larger scales quickly with an exponential decay rate. Conversely, above the critical point, the system follows a strongly attractive limit cycle, which drives and absorbs activity on other scales. Therefore, in both extremes the activity is "trapped" at one scale—it cannot interact with other scales. Conversely, in the immediate vicinity of a critical point small perturbations can grow in magnitude, as the decay rate is much slower, now following a power-law shape. That is, close to the critical point microscopic, respectively, fast, fluctuations have the ability to disseminate to larger, respectively, slower, scales without being damped or

dominated. This ability of activity to "flow" across scales enables stochastic resonance effects and build-up of energy at coarser and slower scales (i.e., synchronized oscillations in slower bands), which increases the correlation between the units. This explanation in terms of optimality of energy transfer is now also reflected in the emerging interest to understand brain dynamics as turbulent-like (Deco and Kringelbach, 2020), as one of the most relevant aspects of turbulence is to facilitate fast energy transfer along a cascade of scales (Frisch and Kolmogorov, 1995).

4. Ghost states

In addition to the functional benefits mentioned above, the loss of stability of fixed-points leads to further interesting dynamical properties, as the phase space close to a bifurcation where stable fixed points become unstable is often governed by latent "ghost" states or "bottle-necks" (Strogatz and Westervelt, 1989), which are characterized by long transients and slow flow (Strogatz, 2018). For example, ghosts can appear after the collision of two fixed points that annihilate each other in a so-called saddle-node bifurcation, leaving a region in phase space that damps trajectories before allowing them to passage out to another fixed point (Strogatz, 2018). Although the system does not exhibit a fixed point at that point in phase space, it mimics the dynamics of a system that possesses an attractor at that point, providing a region in phase space by which the flow is attracted. It is called a ghost, because the attractor is "haunting" the phase space like the ghost of a former attractor: at that point in phase space there does not exist a stable fixed point, but there would be one, if conditions (parameters) were slightly different. An important intuitive consequence of a ghost is that it enables the system to stay for some time in its vicinity, without being "trapped" by it: the system can eventually move away. Such an "escapable" regime with reduced flow leads to slow transients in the vicinity of the ghost state, which makes it possible to create a BNM that slowly oscillates between different states without getting trapped in a fixed-point (Deco and Jirsa, 2012). Furthermore, multistable ghost dynamics provide a model to explain how sudden and intense shifts of brain state can occur even in the absence of underlying parameter changes and, therefore, provide an explanation for the existence of cognitive stability on the one hand, and rapid flexibility and adaptation on the other (Deco and Jirsa, 2012). When the value of inter-areal coupling is just below the critical value for the bifurcation a minor reconfiguration of the network parameters (e.g., related to attention) allows the system to turn a ghost into a genuine attractor and stabilize there to perform a cognitive function, which makes a repertoire of brain states available for rapid activation, even in the absence of any task. For example, the onset of a specific cognitive function may reflect the stabilization of a ghost state through input resulting from sustained attention. Since only a small change of the system is needed to turn a ghost state into a genuine attractor these states can be easily stabilized when needed, which contrasts with a mechanism where stimulus-driven rapid transitions between genuine attractors are assumed. Rather, the long transients implied by ghost states offer the functional benefit of an extended window of response time as well as a form of short-term memory that would not be available for systems that rapidly switch between stable states (Hastings et al., 2018).

5. Limit cycle attractors and subcritical Hopf bifurcations

Up to this point we focused on models that explain how slow (<0.1 Hz) oscillations originate from multistable fixed point dynamics and did not explicitly take the fast (1-100 Hz) oscillations into account that are abundant in empirical activity. These fast oscillations can be modelled by limit cycle attractors (Ashwin et al., 2016). Importantly, limit cycles can form together with fixed-point attractors a multistable phase space, which can be used to simulate the switching of neurons or neural populations between a noisy ground state and a high-power oscillatory mode. For example, Freyer et al. (2011) studied a corticothalamic neural field model that reproduced the bistable switching dynamics of the human

alpha rhythm, which is constantly switching between a noisy ground state and a high-power mode, with dwell times in each mode of up to ~ 20 s. Under this model, the switching between high- and low-power mode corresponds to noise-induced jumps between the fixed-point attractor and the limit-cycle attractor. That is, noise enables to cross the boundaries of the basins of attraction of the two attractors. This spontaneous switching from a noisy, linearly stable, damped oscillation to strong nonlinear periodic oscillations with higher amplitude matches empirical results where it was found that low-power alpha has such a high complexity that it cannot be distinguished from a linear random process while the high power mode was better explained by a nonlinear limit cycle model (Stam et al., 1999). This coexistence of fixed point and limit cycle dynamics, separated by an unstable periodic orbit, occurs in the vicinity of a subcritical Hopf bifurcation, which is characterized by a stable fixed-point becoming unstable and the surrounding unstable spiral becoming absorbed by a stable limit cycle (Izhikevich, 2007). Therefore, the normal form equations for a subcritical Hopf bifurcation, called 'subcritical Hopf model' in the following (while the normal form equations of a supercritical Hopf bifurcation will be called 'supercritical Hopf model'), are a natural candidate for modelling the alpha rhythm, as it is a canonical model for studying multistable transitions between noisy and oscillatory brain dynamics (Freyer et al., 2012).

The subcritical and supercritical Hopf models are, however, quite abstract as their state variables have no direct interpretation in terms of neurophysiological entities like it is the case with neuron models or neural population models where the model structure and associated state variables are designed to be interpreted, for example, as membrane voltages, firing rates or ion channel activities. Therefore, the associated synchronization dynamics and dynamic regimes are more intuitively understood and better relatable to biology using models of biological neural networks that aim to directly represent neurophysiological entities. A typical behavior of biological neurons and their models is that they are in a quiescent state when there is no input but start firing at increasingly higher rates when stimulated with increasing input (Izhikevich, 2007, 2004), which is also reflected in many neural population models (Deco et al., 2008). In terms of dynamical systems, the transition from a spontaneous low-activity (or quiescent) state to large amplitude oscillations corresponds to a fixed point that is rendered unstable by the increasing input current and the stabilization of a limit cycle (Deco et al., 2008). Likewise, in BNMs the transition from the spontaneous fixed-point to a high-activity limit cycle depends on the strength and time delay of network coupling (Ghosh et al., 2008). To understand these effects of coupling strengths and coupling delays on the emergence and stability of sustained oscillations, we consider how two excitatory populations that oscillate in-phase at 10 Hz will reinforce each other when coupled instantaneously: if the coupling strength is large enough the two populations can mutually excite each other, which leads to a self-sustaining oscillation, described by a stable limit cycle in the phase space. Conversely, with a time delay of 50 ms the stable limit cycle becomes unstable, because the signal from the one population now arrives during the antiphase of the other population. For example, Ghosh et al. (2008) studied the stability of a FitzHugh Nagumo-based brain model in dependence of coupling strength and transmission velocity. As in the example with 10 Hz synchronization, the system's stability is relatively unaffected by fast transmission velocities (> 20 m/s), but for a physiologically realistic range of myelinated and unmyelinated axons (1-20 m/s), changes in transmission velocity have strong effects on the system's stability. Likewise, for small coupling strengths the system has a stable low-activity fixed point and only if coupling is gradually increased the fixed-point becomes unstable and oscillatory activity starts. Farther away from this critical region, oscillations are either strongly damped or high-amplitude, resembling pathological activity. Intriguingly, for coupling values that were just below the critical boundary, in between such "pathological" regimes, simulated time series resemble the characteristic transient and spindle-like "waxing and waning" of human alpha-band EEG and MEG. Importantly, the amplitude fluctuation that

was modulated on top of the of the oscillatory (band-limited) time series envelope corresponded to the synchronized slow oscillation of the fMRI signal that was subsequently predicted from the neural time series. This model therefore provided a first mechanistic link between the dynamic waxing and waning of fast neural activity and the slow oscillations in fMRI that underly FC(D), which we will deepen in the following.

6. Multistability in mean-field reductions

To model such a mechanistic link up to the brain level, spiking networks are however impractical, because they come with a large number of free parameters and this complexity limits their efficiency for simulating entire brains (Jordan et al., 2018). Therefore, and to make them more amendable to analytical and numerical treatment, the central insights created by their study are condensed and simplified to build so-called neural mass or mean-field models (Deco et al., 2008).

In BNMs that are based on spiking networks (Deco et al., 2013; Deco and Jirsa, 2012; Ghosh et al., 2008) the decisive element for the best fit with empirical FC was the tuning of the system to a critical point where the low firing attractor became unstable. Importantly, this dynamical regime for the emergence of slow correlated oscillations can not only be produced from the bottom up in realistically coupled integrate-and-fire spiking networks, but it can also be captured by reductions made by mean field approximations, and even by further linear simplifications (Deco et al., 2008). Mean-field analysis with diffusion approximation simplifies synaptic input terms under the assumption that network activity fluctuates around a stationary state with constant population firing and synaptic currents, which yields a much simpler model that nevertheless reproduces the essential attractor dynamics and that can be integrated much quicker than the full spiking network (Brunel and Wang, 2001). Several reductions of the realistic spiking models down to a linearized variant (Deco et al., 2013) all showed qualitatively identical dynamical properties and were all able to (fairly) predict static FC, indicating that linear interaction is sufficient to explain important characteristics of the network pattern of static FC. In addition, with simplified models the network's covariance can be analytically calculated from the eigenvectors of the system's Jacobian matrix, which provides a direct analytical link between static FC, SC and dynamics (Deco et al., 2013). This analysis indicates, as expected from numerical simulation of spiking and reduced models, that static FC can be interpreted as a function of an individual's SC (Deco et al., 2013).

7. Multistability and functional connectivity dynamics

Up to now we reviewed explanations for the emergence of static FC and found that the best predictions in the previously discussed models (Deco et al., 2013; Deco and Jirsa, 2012) and similar models (Deco et al., 2009; Ghosh et al., 2008) have occurred near a bifurcation where the spontaneous low-firing state of the network became unstable and firing moved towards higher values. However, in contrast to static FC, the best prediction of FCD with a multistable model was not found near the bifurcation where the spontaneous state became unstable. Hansen et al. (2015) used a slightly different parameterization (higher excitatory recurrence, higher noise, lower global coupling) that yielded up to six instead of two firing rate attractors in the dynamic mean field reduction of the discussed spiking model (Deco et al., 2013). This parameterization had the important effect that now a bistability was directly implemented in uncoupled units: an additional fixed-point attractor allowed uncoupled units to assume a high-firing state without the need for slow reverberating excitatory inputs from the global network. Importantly, the working point optimized to fit static FC is not the same that optimized fit with FCD (to optimize FCD the Kolmogorov-Smirnov distance between empirical and simulated FCD distributions was minimized). Under this slightly differently parameterized model the optimal working point for predicting static FC was still close to a critical point where the spontaneous state became unstable. However, at

the optimal working point for FC no stable dFC patterns emerged and no dFC switching occurred. Rather, the best fit with FCD occurred at a lower value for global coupling where the simulated dFCs were less constrained by SC and showed complex non-trivial patterns, strongly reminiscent of RSN topologies. While the pattern of the static FC still correlated strongly with SC, dFCs showed a richer repertoire of patterns that were quite dissimilar to the SC pattern, but which were transiently stable enough to enable a better reproduction of the checkerboard pattern found in empirical FCD maps. The emergence of these additional attractor states required an interplay between local and collective dynamics that led to the emergence of six new firing-rate attractors, which were not observed with the simpler variants of this model that did not have a local bistability in uncoupled units. In this BNM the model's state continuously sampled the rich dynamical repertoire of a complex multi-attractor multistable phase space. This sampling is characterized by short periods of dwelling in the basins of attraction of the different attractors interleaved with ongoing switching between them. Although the system is constantly attempting to converge towards one of its six fixed points, it is constantly pushed out of these equilibria by noise, which enables to sample the different subspaces. The ongoing movement either towards a fixed-point or escaping towards a different attractor gives rise to a dynamic itinerancy characterized by transient states that never settle in an equilibrium. This ongoing multistable switching between states is similar to metastable dynamics, which are discussed in the following.

8. Metastability and intermittent synchronization

In contrast to stable attractor states metastable states are stable only on short timescales and metastable systems have solutions that spend a long time in a state that changes extremely slowly, but that is far from a stable or unstable stationary solution (Carr and Pego, 1990; Fusco and Hale, 1989). While metastable states are characterized by a very slow evolution, they can be connected to other metastable states through intermittent periods of fast motion (Fusco and Hale, 1989). Importantly, metastable states can be linked into a sequence of intermittently stabilizing states, so-called heteroclinic cycles, along which the system wanders, but never ultimately settles (Afraimovich et al., 2004). Heteroclinic cycles are therefore an attractive model to understand the contradictory requirements of cognitive functions like learning and decision-making in a changing environment: they need to be robust and reproducible on the one hand, but sensitive and flexible on the other hand (Kelso, 2012; Rabinovich et al., 2008). In neural models of weakly coupled oscillators metastability can, for example, be observed as slowly alternating epochs of intermittent phase synchronization and desynchronization between the units (Honey et al., 2007). At weak coupling levels such a system of coupled oscillators never settles in a steady state but instead a large number of metastable states with complex multiscale temporal structure emerges. An important take-away from this study is that the ongoing fluctuation of the degree of synchronization between populations on the fast time scale gives rise to oscillations on a slower time scale. That is, the fast neural dynamics of different brain regions exhibited intermittent synchronization and desynchronization on a time scale of hundreds of milliseconds with epochs of synchronization typically lasting between 50 and 300 msec, which is consistent with *in vivo* observations (Varela et al., 2001). Importantly, this ongoing modulation of synchronization patterns—slow variations in the statistics of intermittent coupling and decoupling—determined the emerging BOLD amplitude and the correlation between BOLD signals and hence the FC pattern. Further analysis showed that the strengths of functional connections in FC matrices, the BOLD signal amplitude and the strength of synchrony of fast activity between different brain regions were strongly correlated, pointing towards a common origin: region pairs that engaged in long synchronous episodes tended to have a stronger FC and elevated BOLD amplitude (Honey et al., 2007).

In other words, the intermittent synchronization mechanism identifies the origin of the slow fluctuation of fMRI dFC (<0.1 Hz) as a re-

sult from the fluctuation of transient coupling on a much faster time scale (~10 Hz), but with a lag of about 2-4 s due to hemodynamic delays. This theoretical result provides an explanation for empirical observations that show that large-scale networks in MEG can be well described by recurring visits to short-lived transient network states (50–200 ms) that have characteristic patterns of intermittently synchronized power envelopes (Baker et al., 2014) and phase coupling time series (Vidaurre et al., 2018) that correspond well with the topography and switching of resting-state networks in fMRI. These studies suggest that spontaneous brain activity can be broken down into distinct network patterns that are stable for periods of 50 to 200 ms and that these transient states reflect the temporal switching of FCD (Baker et al., 2014). Consistent with earlier results that show the similarity of spatial networks in fMRI (Beckmann et al., 2005; Smith et al., 2009) and temporal networks in MEG (Brookes et al., 2011) these observations support the idea that functional brain networks derive from the sequential activation of a set of metastable brain states rather than having stable attractors (Tognoli and Kelso, 2014).

9. Chimera states and slowed collective synchronization

Metastable intermittent synchronization can also explain amplitude envelope FC and FCD observed in alpha- and beta-band (~8–30 Hz) MEG, which itself has a strong correspondence with fMRI FC (Brookes et al., 2011; Hipp et al., 2012). In a Kuramoto-based BNM (Cabral et al., 2014) uncoupled units were set to oscillate at 40 Hz, which is a reasonable resonant frequency of neural masses following electrophysiological (Buhl et al., 1998) and theoretical (Brunel and Wang, 2003) results. Time-delayed coupling near a critical working point led to an ongoing fluctuation of intermittent synchronization and desynchronization between subsets of nodes, forming and dissolving of metastable coalitions. Interestingly, under this model the slow oscillation was not modulated on top of the intrinsic fast oscillation of the uncoupled units (amplitude envelope fluctuation); rather, the 40 Hz oscillators temporarily synchronized at slower delay-dependent network frequencies with a peak in the alpha/beta band due to the presence of coupling delays on the order of 10 ms. More specifically, the dynamics of the model alternated between their intrinsic limit cycle at 40 Hz and slow collective limit-cycles of synchronized sub-networks, which are slowed due to the time delays of signal transmission between brain areas (Niebur et al., 1991). Epochs of strong synchronization (ergo, high correlation; ergo, high dFC) were characterized by bursts of high-power activity in frequency bands much lower (10–20 Hz) than the intrinsic frequency of 40 Hz. This coexistence of synchronized and desynchronized domains in a network are called 'chimera' states and it is unexpected to find such a break of symmetry in identical oscillators with symmetric coupling (Abrams et al., 2008). Importantly, synchronization is strongest in the slow (<0.1 Hz) amplitude envelope fluctuation of band-pass (alpha, beta, gamma bands) filtered node time series, which matches the time scales of envelope fluctuations observed in empirical MEG data (Brookes et al., 2011; Hipp et al., 2012). In summary, in a metastable regime subnetworks of fast limit-cycle oscillators have the ability to spontaneously synchronize and desynchronize on a slow time scale and this fluctuation in the degree of synchrony explains the correlated slow BOLD-signal fluctuations underlying fMRI BOLD FC (Deco et al., 2009) and MEG envelope FC (Cabral et al., 2014).

10. Slow oscillations by pulsed inhibition

While the previous model agrees with the empirically observed positive correlation between gamma band activity and BOLD fMRI (Logothetis et al., 2001), as well as the negative correlation between alpha activity and BOLD fMRI (Goldman et al., 2002; Laufs et al., 2003; Moosmann et al., 2003; Ritter et al., 2009), it does not provide a direct mechanistic explanation why the switch from fast oscillations to slower oscillations leads to reduced energy requirements and

metabolic demands that would explain the decrease of neural firing and the BOLD fMRI amplitude during high alpha activity (Kilner et al., 2005; Schirner et al., 2018). By injecting EEG that was simultaneously acquired with fMRI into the excitatory and inhibitory populations of a BNM, a mechanism was inferred that directly links ongoing alpha activity modulation with the slow hemodynamic oscillations observed in resting-state fMRI (Schirner et al., 2018). The injected source-localized EEG data drove BNM dynamics such that simulation results not only predicted FC patterns, but also the underlying empirical fMRI time series, which were used to fit the model. Although the model was fit to the slow fMRI time series dynamics, it helped explain activity on much faster time scales, like the anticorrelation between individual alpha phase cycles and firing rates (Haegens et al., 2011) and their relationship with the ongoing balance of excitatory and inhibitory currents (Atallah and Scanziani, 2009). Importantly, the identified mechanism of this model postulates that intermittent bursts of high-power alpha activity led to pulses of inhibition that reduce the recurrent build-up of excitation in the global brain network, which leads to a phasic decrease of the ongoing firing of excitatory populations. The ongoing waxing-and-waning of alpha power and its effect on neural firing then led to slow resting-state oscillations as observed in fMRI. Taken together, this and the previously discussed mechanism of slowed collective synchronization (Cabral et al., 2014) may explain the positive relationship between gamma power and BOLD amplitude as well as the inverse relationship between alpha power and BOLD amplitude: gamma power decreases and alpha power increases when gamma oscillators synchronize at a slow collective alpha rhythm (Cabral et al., 2014); the increased alpha power in turn leads to an inhibition of neural firing and the reduced energetic demands lead to decreased BOLD amplitude (Schirner et al., 2018).

11. Metastability near a supercritical HOPF bifurcation

Multistable and metastable dynamics were both used to explain the emergence of FC(D) in the models discussed above. To better isolate the question which kind of dynamics better explains FC(D) we now turn towards Landau-Stuart oscillators, which describe the dynamics of a system near a supercritical Hopf bifurcation, where the system switches between damped oscillations around a fixed-point and sustained limit-cycle oscillation (Izhikevich, 2007). This model enables to study the dynamic principles underlying the emergence of FC(D) in a more direct manner, as a single parameter controls whether the system is governed by a multistable regime on either side of the bifurcation or a metastable regime at the bifurcation point (Freyer et al., 2012; Vlachos, 1995). For example, Deco et al. (2017b) studied a brain model based on Landau-Stuart oscillators where the intrinsic frequency of all network nodes was set into the range of the 0.04–0.07 Hz band of slow fMRI oscillations, which is interesting as it isolates those aspects of FC and FCD that can be readily explained by slow processes without the need for faster activity. Interestingly, analysis of model dynamics revealed an important advantage of metastable regimes in comparison to multistable regimes (Hansen et al., 2015). For the existing multistable model the optimal working point of global network strength for predicting FCD distributions was at a different value than the optimal working point that optimally predicts static FC (Hansen et al., 2015), which is implausible, because FC and FCD co-occur in empirical data where dFC matrices can be computed from a sliding window analysis of the longer time series underlying static FC (Hutchison et al., 2013). Conversely, the metastable dynamics of the Landau-Stuart oscillators at a supercritical Hopf bifurcation enabled to simultaneously optimize the fit with static FC and FCD (Deco et al., 2017b). Importantly, at the optimal working point at the bifurcation not only FCD fit peaked, but also the variability of synchronization patterns—used as an indicator of metastability—was maximized and at the closest to its empirical value. While a wide range of global coupling values predicted static FC equally well, the fit with FCD peaked only within a relatively narrow range, which makes it a candidate metric for model optimization. This model, therefore, provides

strong corroboration for metastability as the underlying FCD mechanism, since here a single parameter allows for a smooth transition between and direct comparison of multistable versus metastable dynamics. Comparing model dynamics for attractor dynamics (fixed point for negative values of the bifurcation parameter, and limit cycle oscillations for positive values) versus metastable dynamics at the bifurcation between the attractor states (bifurcation parameter equals zero) shows a clear superiority of the metastable state to describe FCD. Importantly, what distinguishes the multistable from the metastable regime is that in the former the synchrony (phase uniformity) between nodes remained relatively stable while in the metastable regime there was more variance and switching between synchronized and desynchronized clusters. Interestingly, the best fit occurred at the edge of the Hopf bifurcation, close to the value zero for the bifurcation parameter, but still on the negative side, such that oscillations were still damped. The produced time series at this working point therefore also showed more plausible waveforms and spectral contents than previous models: neither a sustained oscillation (as it is for example the case with Wilson-Cowan and Kuramoto units), nor the "filtered noise" spectrum resulting from fixed point attractor dynamics that lacks a clear peak at a dominant frequency. Rather, a mixture of the two emerged: the time series had a chaotic and high-dimensional appearance, like noise, but with a dominant oscillatory component around 0.05 Hz, visually similar to resting-state fMRI time series (He, 2011). In summary, Landau-Stuart oscillators allow a more direct comparison of multistable and metastable dynamics within a single model, underlining the superiority of metastable dynamics to predict FCD. The involved simplifications come, however, with a drawback: the model does not help to explain how the slow oscillations emerge and what their relationship is with the faster frequency content of neural power spectra.

12. Plausible power spectra

Current BNMs generally fail to adequately replicate the complex fractal shape of EEG or MEG spectra (Messé et al., 2015). Empirical spectra have a scale-free $1/f$ shape (power is inversely proportional to frequency) with defined peaks, e.g., in the alpha range during wakeful rest or in the delta range during deep sleep (Linkenkaer-Hansen et al., 2001). Neural models typically produce either "filtered noise" (the injected noise "filtered" by the fixed-point dynamics), pure oscillations (in limit cycle models), or noisy metastable oscillations, all of which do not address all of the salient characteristics of empirical power spectra (Messé et al., 2015). Although the delay-dependent slowed collective synchronization reviewed above is an intriguing mechanism to explain how limit cycle oscillators could produce a variety of collective oscillation frequencies, the produced time series of existing models still show implausible waveforms with strong individual peaks in the spectrum and a lack of power in other bands preventing to form the characteristic $1/f$ shape (Cabral et al., 2014). Problematically, most models assume a single homogeneous oscillation frequency in every brain area (Deco et al., 2017a). In contrast, when comparing empirical electrophysiological and fMRI data there are multiple "carrier" bands for FC and FCD (Brookes et al., 2011; Hipp et al., 2012) and their amplitude envelopes show a rich correlation structure (that is, FC) over a wide range of different frequency bands from 2 to 128 Hz that are strongly correlated with fMRI FC (Hipp and Siegel, 2015). Interestingly, electrophysiological oscillations showed primarily connection-specific and not network-specific correlations with the BOLD signal indicating that BOLD networks reflect a mixture of neuronal activity oscillations across different frequency bands rather than being linked to individual specific frequencies (Hipp and Siegel, 2015).

Problematically, a neural model with a single oscillatory frequency only produces envelope correlations in that single band while there is not much power in the other bands (Deco et al., 2017a). Consequently, amplitude envelope FC is restricted to a frequency band closely located around the fundamental frequency of the uncoupled oscillators and does

not explain envelope dynamics in the other frequency bands, as observed with MEG and EEG.

To produce more plausible spectra and band-specific envelope FC, Deco et al. (2017a) used seven Landau-Stuart oscillators that were set to different fundamental frequencies (4, 8, 12, 16, 20, 24 and 28 Hz) to simulate each brain region. Here the oscillations in the different bands acted as carrier waves onto which slow power fluctuations were modulated, which enabled to predict amplitude envelope FC in all bands, better resembling empirical data. However, because the same SC matrix is used to connect the oscillators at different frequencies, there is little diversity in the pattern of envelope FCs at different frequencies, which is in contrast to empirical data that shows that different rhythms show distinct FC topographies (Hipp and Siegel, 2015; Vezoli et al., 2021). Furthermore, under this model, where no coupling between oscillators at different frequencies exists, no cross-frequency interactions like amplitude-to-amplitude, phase-to-phase or phase-to-amplitude coupling emerged, which is in conflict with empirical literature (Engel et al., 2013). In summary, although the model addressed the BNM problem of implausible power spectra, it is an open question in how far stacks of oscillators are a plausible model for explaining the spectrum of brain waves, as such stacks would correspond to brain areas that would resonate in parallel at a range of different frequencies. An alternative hypothesis is that the $1/f$ shape emerges from neurons simultaneously synchronizing at a multiplicity of different delay-dependent network frequencies, similar to what is proposed in the Cabral et al. (2014) model reviewed above, but with a more broader distribution of emerging delay-dependent frequencies, which would probably require a much more complex neurocircuitry and delay architecture.

13. Intermittent synchronization and communication through coherence

Empirical and modelling results indicate that intermittent synchronization may have important functional benefits for gating interareal communication. For example, the influential 'Communication through Coherence' (CTC) theory (Fries, 2015, 2005) posits that neuronal communication is subserved by rhythmic synchronization as this creates alternating epochs of excitation and inhibition that focus both spike output and sensitivity to input into narrow temporal windows. Excitatory (inhibitory) inputs that arrive consistently during periods of excitation (inhibition), have a higher chance of triggering (preventing) postsynaptic spikes compared to inputs that arrive at random times and therefore increase effective connectivity, that is, the directed influence one population exerts over another population. Consequently, a population that receives inputs from several different populations responds primarily to those with which it is synchronized, which makes neural communication selective and allows for precise and flexible routing of information while maintaining the same underlying skeleton of anatomical connections. The theory received experimental support, for example, from studies that show that rhythmic activity modulates input gain (Siegle et al., 2014; van Elswijk et al., 2010), that strong effective connectivity requires coherence (Womelsdorf et al., 2007), and that selective communication is implemented through selective coherence (Schoffelen et al., 2011). Complementary modelling results show that circuits that exhibit intermittent synchronization display emerging frequency entrainment and phase locking that determine the direction of information flow, as predicted by the CTC theory (Palmigiano et al., 2017). In this study spontaneous short-lived bursts of gamma synchronization were produced by coupling individual units that were tuned below the onset of stable oscillatory synchrony. The resulting transient epochs of coherence then either boosted or suppressed information transfer, depending on the transient phase relationship between the involved units, enabling to selectively gate information flow along different pathways. Crucial for the emergence of effective inter-areal communication was, again, the tuning of the coupling strength parameter to a weakly-coupled state in between trivial fully asynchronous or synchronous

states, similar to the emergence of FC(D) in the models discussed above.

Studying CTC in brain models in this manner reveals a striking relevance of both, intermittent synchronization and metastability, for both, functional connectivity and effective connectivity (Deco and Kringelbach, 2016). As we discussed earlier, tuning a brain model close to a supercritical Hopf bifurcation not only maximized FC(D) fit, but also the system's metastability, characterized as the variability of phase-locking synchronization patterns between different nodes (Deco et al., 2017b). This observation is non-trivial as a broad and diverse number of phase-coupling states between different network nodes is equivalent to a broad and diverse set of channels for communication through phase synchronization. In other words, a large repertoire of intermittently stable phase relationships gives rise to a large repertoire of CTC-like communication routes. Consequently, maximizing metastability in this manner simultaneously maximizes the ability for flexible and effective communication in static brain networks, which supports the idea that healthy brain dynamics maximize metastability in order to support flexible communication between areas, while a more limited repertoire of CTC channels would lead to neurocognitive impairments (Deco and Kringelbach, 2016).

14. Conclusion

After comparing the different mechanisms underlying the different models in this review, it is becoming clearer that for creating viable theories of FC(D) it is not enough to "blindly" fit dynamic models with individual metrics of empirical FC(D) and then selecting that with the highest fit. The value of BNMs is that they seek to simulate actual physiological entities like firing rates, membrane potentials or BOLD time series, with the idea that by analyzing their behavior researchers can discover underlying physiological mechanisms. None of the individual models provided a full picture that integrated all the important details, but rather pointed to certain pieces of the puzzle. The differences between the models are the assumptions and simplifications on which they are built. For example, Kuramoto-based models helped to create hypotheses on the formation of structured envelope oscillations and delay-dependent slowed synchronization (Cabral et al., 2014) that are, thanks to their simplicity, amenable for analytic study. However, the link between phenomenological oscillators and neural biophysics is not clear as they are built on the assumption that brain areas are constantly engaged in self-sustained oscillations, as even uncoupled units are constantly oscillating at their set intrinsic frequency, without providing a mechanism that would explain the origin of this oscillation, which requires more detailed neuron-level models. By addressing the problem from different perspectives, different models provide different mechanistic information that may be useful to build an overall theory.

In this context, the question "multi- or metastable?" (or multistable switching between metastable cycles?) seems not so important, because, as we have seen, the same system could be characterized as both, multistable or metastable, depending on what aspects of the system were chosen as the relevant state variables, control parameters, etc. When we talk about multistability we primarily mean that there appear states that we identified as "stable" and attractive, which corresponds in the brain to population activity that supports itself through reverberating inputs. However, what appears more crucial is the ongoing ability of the system to *destabilize* in order to induce the itinerant dynamics of functional brain networks, which is then cast into different dynamic processes like multistable noise-driven switching, noise-driven exploration of the vicinity of an attractor, reconfiguring the attractor landscape via parameter changes or wandering along heteroclinic orbits. The decisive element in successful models of FCD—e.g., the multistable model of Hansen et al. (2015) and the metastable model of Deco et al. (2017b)—seems to be the existence of many different (semi-)stable states. In Hansen et al. (2015) the best prediction happened at the working point of the model where the highest number of multistable states emerged in

the network. Similarly, in Deco et al. (2017b) the best FCD prediction happened at the point where the variability of the number of states of phase synchrony was maximized. In this light, the question of whether subspaces are stable or unstable—or whether their stability can be flexibly reconfigured—seems less important than the number of states and the combined dynamic repertoire that they are able to provide. And more important even than the number of states is the functions they encode, which are in the currently existing BNMs arguably simple. Therefore, it appears promising to better understand how low-dimensional subspaces that constrain the system's flow (and thereby the possible functional configurations of the system), called structured flows on manifolds (McIntosh and Jirsa, 2019), could be designed in a targeted manner, e.g. by using circuit training algorithms (Zenke and Vogels, 2021). Promising are also studies where BNMs are equipped with the more complex dynamics of so-called strange attractors (which exhibit a fractal structure, alluring to scale invariance), which yielded good predictions of both FC and FCD, similar to the supercritical Hopf model, but over a wider range of parameters (Piccinini et al., 2021).

What are the next steps? Predicting static FC from SC with BNMs is not an overly complex task—even simple linear models can predict the pattern to a fair degree (Cabral et al., 2017). On the other hand, predicting plausible itinerant switching dynamics of FCD is much harder. There exist successful models to explain the histogram of FCD, phase synchronization, metastability (meaning "variability"), slow oscillations and synchronization patterns. However, an open question is in how far the actual repertoire of dFC patterns and their explicit switching dynamics can be reproduced, as fitting only the FCD distribution conveys no information about the plausibility of the dFC patterns or their sequence of switching. Also, what is missing is a model that predicts dFCs and FCD on the basis of plausible neural activity. The power spectra of BNM simulations look implausible—either filtered noise or overly dominant oscillations—and do not reproduce the characteristic shape of empirical spectra (1/f slope with a waxing-and-waning peak in the alpha range and ongoing short-lived power modulations in lower and higher bands), even those that are based on spiking networks (Cabral et al., 2017; Messé et al., 2015). Here, too, the goal is not an exact quantitative reproduction but rather explaining key qualities and the underlying mechanisms leading to their emergence. Different models reproduce different aspects of the desired power spectra, so failure to reproduce could be related to the simplifications in these models. One key question, for example, is that on the emergence of slower rhythms (e.g., alpha and beta bands), as well as their ongoing power modulation. One hypothesis posits that slow oscillations emerge from metastable chimera synchronization as in Cabral et al. (2014) where fast oscillators (40 Hz) spontaneously synchronized on a slower network limit cycle in the alpha and beta band range. An alternative hypothesis is provided through the model of Freyer et al. (2011) where a slow multistable switching of the alpha rhythm power emerged at a subcritical Hopf bifurcation, reproducing detailed empirical observations. Neither of the two hypotheses can explain the full complexity of empirical data, but they nevertheless help to elucidate candidate mechanisms that can be used to refine and constrain more detailed models and to design empirical experiments. A parsimonious way forward may be multiscale simulations where the majority of the brain are simulated with simple models and more details are only incorporated at selected regions of interest (Meier et al., 2021). Likewise, simulations can also be simplified by not directly modelling all aspects of brain activity, but instead injecting empirical data (e.g., source projected EEG or MEG, or artificially generated plausible activity) into the population models (Schirner et al., 2018).

Having traced the origins of FC(D) to synchronization of coupled oscillators, we may ask: what is this tendency of neural populations to synchronize good for, anyway? Apart from the already mentioned advantages of systems near a critical point (regarding improved communication, increased repertoire of states, information capacity and dynamic range) the function of synchronization and network-formation may be related to 'predictive coding' theories. Predictive coding assumes that

the brain is encoding a model of the world that is used to predict sensory inputs in order to adapt behavior and to update the model based on prediction errors (Fiser et al., 2010; Rao and Ballard, 1999). The link to predictive coding is important as there is a remarkable correspondence between the anatomical connectivity of canonical cortical microcircuitry, its tendency for synchronization in different frequency bands, and the dynamical constraints implied by predictive coding (Bastos et al., 2012). Specifically, the predictive coding model predicts that the frequency of oscillatory activity of superficial pyramidal cells for encoding prediction errors is suppressed when passing prediction errors to deep pyramidal cells (Friston, 2008), which is in close agreement with empirical data that showed that gamma-band synchrony was largely confined to superficial layers whereas deep layers showed maximal coherence in theta and alpha ranges (Bosman et al., 2012; Buffalo et al., 2011). The resulting functional implications of such concurrent synchronization with different rhythms have been formulated in the Communication through Coherence hypothesis, which posits that the faster bottom-up gamma rhythms selectively focus synaptic inputs to arrive simultaneously by entraining the rhythm between pre- and postsynaptic neurons, while the slower alpha-beta band top-down rhythms implements an attentional sampling of different inputs or representations (Fries, 2015). Extending this idea beyond the skull, the function of synchronization for predictive coding could be one of creating a resonance effect between internally generated (e.g., memory-dependent) activity fluctuations and activity fluctuations originating outside the brain, arriving in the form of external stimuli (Berkes et al., 2011). Under this theory, perception could induce dynamical instabilities and associated critical slowing that enable the brain to respond sensitively to sensory perturbations to aid active inference (Friston et al., 2012).

Implementing predictive coding, e.g., with the help of orchestrated plasticity rules, and gradients of excitation versus inhibition (Wang, 2020), to shape a hierarchical topology that supports exchange of predictions and prediction errors between higher and lower areas (Kanai et al., 2015), could pave the way for brain models that self-learn complex functions from supplied inputs (Zenke et al., 2015).

The idea that synchronization is part of a general mechanism for perception, communication and adaptation that extends even beyond the individual receives impressive support by a growing number of experiments that revealed the existence of synchronized fMRI activity as well as synchronized dFC fluctuations across participants that can be reliably linked with visual, auditive or even narrative features of complex "free viewing" naturalistic stimuli like watching a movie (Betzel et al., 2020; Bolton et al., 2019; Hasson et al., 2004; Manning et al., 2018; Simony et al., 2016). Out of this perspective the question may follow: how are functional networks and synchronization related to cognitive content like thoughts and other mental activity? On the one hand there is compelling evidence that BOLD dFC is sensitive to ongoing cognitive and behavioral tasks and states (Cohen, 2018; Gonzalez-Castillo and Bandettini, 2018; Lurie et al., 2020; Shine and Poldrack, 2018). Importantly, classifiers trained on dFC patterns during task execution can be used to predict subjective emotional experience, objective measures of task performance, task epoch, condition-specific pretrial preparatory processes, subsequent behavioral performance and perceptual outcomes (Lurie et al., 2020). For example, it has been possible to accurately track the mental state of subjects that engaged in and transitioned between different externally cued tasks for time windows ranging from 180 s to 22.5 s and at the same time a significant association between classification performance and behavioral performance was demonstrated (Gonzalez-Castillo et al., 2015). Similarly, in the absence of task instructions or stimulation spontaneous BOLD activity and network dynamics can also be closely associated with self-reported thoughts and other features of ongoing mind wandering (Chou et al., 2017; Kucyi, 2018; Kucyi and Davis, 2014; Mittner et al., 2014). On the other hand, the conclusion drawn from these observations that all ongoing BOLD activity directly reflects cognition and behavior can be easily challenged (Laumann and Snyder, 2021) as FC topography remains remarkably sta-

ble during slow-wave sleep (Sämman et al., 2011), anesthesia (although covariance diminishes with increased sedation; (Mhuircheartaigh et al., 2010)), task state (Gratton et al., 2018), over long scanning times (Poldrack et al., 2015), across scanning sessions (Gratton et al., 2018), across humans (Damoiseaux et al., 2006), and even across mammalian species (Hutchison et al., 2010; Mantini et al., 2011). A more nuanced perspective therefore acknowledges that brain activity may not only be for "online" thinking processes, but may also include "offline" processes such as homeostatic and consolidative signaling related to learning and memory (Laumann and Snyder, 2021). Especially ongoing fluctuations of arousal have been associated with global waves of activity that slowly propagate in parallel throughout the brain and that likely account for a large portion of variance in FCD and synchronization dynamics (Lurie et al., 2020; Raut et al., 2021).

In summary, BNMs helped to understand important aspects of *resting-state* FC(D) in terms of *relatively* simple dynamical primitives (in comparison to the much more complex behavior of strange attractors). Now it seems high time to equip BNMs with more complex function, for example, by first learning the structure of low-dimensional manifolds from empirical data (Gallego et al., 2020; Rué-Queralt et al., 2021) and then implementing them into small-scale and large-scale networks (McIntosh and Jirsa, 2019; Zenke and Vogels, 2021).

Data and code availability

The data and code used in this article can be downloaded from https://github.com/BrainModes/Review_DynamicPrimitives.

Credit authorship contribution statement

Michael Schirner: Conceptualization, Visualization, Writing – original draft, Writing – review & editing. **Xiaolu Kong:** Resources, Writing – original draft, Writing – review & editing. **B.T. Thomas Yeo:** Resources, Writing – original draft, Writing – review & editing. **Gustavo Deco:** Conceptualization, Writing – review & editing, Resources, Writing – original draft. **Petra Ritter:** Conceptualization, Resources, Writing – original draft, Writing – review & editing.

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