Dynamical correlation patterns and corresponding community structure in neural spontaneous activity at criticality

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Abstract It has been considered that the state in the vicinity of a critical point, which is the point between ordered and disordered states, can underlie and facilitate information processing of the brain in various aspects. In this research, we numerically study the influence of criticality on one aspect of brain information processing, i.e., the community structure, which is an important characteristic of complex networks. We examine community structure of the functional connectivity in simulated brain spontaneous activity, which is based on dynamical correlations between neural activity patterns at different positions. The brain spontaneous activity is simulated by a neural field model whose parameter covers subcritical, critical, and supercritical regions. Then, the corresponding dynamical correlation patterns and community structure are compared. In the critical region, we found some distinctive properties, namely high correlation and correlation switching, high modularity and a low number of modules, high stability of the dynamical functional connectivity, and moderate flexibility of the community structure across temporal scales. We also discuss how these characteristics might improve information processing of the brain.

Keywords Criticality · Neural fields · Brain spontaneous activity · Functional networks · Community structure

Introduction

In the field of complex systems, critical phenomena are a topic of interest because of their distinct properties. The

phenomena occur at the point of second-order phase transition (continuous type), which is called the critical point. The special properties that distinguish critical phenomena are divergence of correlation length, scale invariance, and power-law distributions of certain variables. There are many phenomena in nature that are thought to be related to criticality, such as earthquakes (Sornette and Sornette 1989) and solar flares (Lu and Hamilton 1991).

For the brain and the neural system, many studies have conjectured that the brain performs its tasks and processes information in the critical regime, which Beggs (2008) referred to as the criticality hypothesis. For example, simulations have demonstrated that the dynamic range (Kinouchi and Copelli 2006), memory capacity (Haldeman and Beggs 2005), and computational power (Bertschinger and Natschläger 2004) of neural networks are maximized at a critical point. Another numerical study demonstrated that neural activity in a critical regime is able to synchronize with each other more efficiently (Termsaithong et al. 2012). Furthermore, a critical neural network is able to flexibly respond and adapt to stimuli, which is crucial for a learning process (de Arcangelis and Herrmann 2010). This hypothesis is also supported by findings of certain empirical experiments, e.g., neuronal avalanches (Beggs and Plenz 2003; Petermann et al. 2009; Hahn et al. 2010) and $1/f$ -type power spectra from various kinds of neural activity measurements (Henrie and Shapley 2005; Freeman et al. 2000; Thurner et al. 2003).

Even in a resting state, i.e., with no explicit input or performance of a task, the brain is actually not at rest but constantly activated. This is called brain spontaneous activity or ongoing activity. It consumes most of the brain energy, while task-related activity requires much less energy (Fox and Raichle 2007). This fact underlines the importance of the brain spontaneous activity even though its functions are still ambiguous. It was shown that the

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spontaneous activity patterns in brain regions that belong to the same cognitive systems (Fox and Raichle 2007; Biswal et al. 1995; Hampson et al. 2002; Cordes et al. 2001) or perform similar task-evoked activity (Fox and Raichle 2007; Greicius et al. 2003) are correlated. It was also found that there is an anticorrelation between the spontaneous activity of positive and negative task-responsive networks (Fox et al. 2005). Adopting the graph theoretical framework, we can construct the functional connectivity network from neural activity association, such as correlation (Biswal et al. 1995; Lowe et al. 1998), and then we can study the topological properties of the graph or network (Bullmore and Sporns 2009).

In this research, we numerically studied correlation patterns and functional network structure of simulated brain spontaneous activity in a critical regime using a neural field model. Then, we compared the results with those of other regimes, namely, subcritical and supercritical. The network property investigated in this research is the modularity or community structure, which characterizes how well the network organizes into modules or communities. In other words, community structure is composed of node groups in the network such that connections within each group are denser than those between groups. Modularity is one of the characteristics of a complex network (He et al. 2009), allowing the network to organize an internally distributed structure. For example, communities of metabolic networks are established by functional descriptions, and those of citation networks are based on research topics.

Some studies have considered community structure in functional connectivity of brain spontaneous activity and demonstrated that this functional network possesses highly modular structure (He et al. 2009; Ferrarini et al. 2009; Meunier et al. 2009). Although a functional network measured in a long timescale reflects an underlying structural network, in a short timescale, a functional network deviates significantly from a structural network and is much less constrained by structural connectivity (Honey et al. 2007). In addition, some researchers found that the correlation between spontaneous activity patterns across the brain is not static (Chang and Glover 2010; Park et al. 2012). It can change with time and make the corresponding functional connectivity dynamic as well. Therefore, in this study, we focus on the dynamics of the correlation and functional network of neural activity.

Methods

Neural field model

Neural fields are mesoscopic models that describe the dynamics of a local neural population activity in a spatially

extended system. Each point in the field represents the total activity of neural populations in the vicinity of that point. Its dynamics depends on the internal dynamics, activity of other points weighted by synaptic efficacy, and occasionally, an external stimulus. A general form of the neural field equation (Amari 1977) is the integro-differential equation given as follows:

$$\frac{1}{\alpha} \frac{\partial u(x, t)}{\partial t} = -u(x, t) + \int_{-\infty}^{\infty} w(x - y) f(u(y, t)) dy, \quad (1)$$

where $u(x, t)$ is the neural activity at point x and time t ; α is the decay rate of the activity; $w(x)$ is a weight function that defines the strength of connections between each pair of points in the field; and $f(x)$ is a firing rate function, for a given activity input, that determines the firing rate output transmitted to postsynaptic neurons. Note that this equation describes a simple form of the neural field without an external input and transmission delay. The first term on the right-hand side of Eq. (1) represents decay dynamics of the activity, while the second term represents the effects of output from other neural populations.

There are many reasonable options for $w(x)$ and $f(x)$. However, the firing rate function $f(x)$ should be monotonically non-decreasing and saturate to a certain maximum rate. In this research, we select

$$w(x) = (c - d|x|)e^{-b|x|}, \quad (2)$$

where $c = 1$, $d = 1/2$, and $b = 1$ in the following analysis. This function is called a Mexican hat or a wizard hat function because of its shape. This shape of the weight function features short-range excitation and long-range inhibition, which is one of common weight functions widely used in neural field study. By assuming that a neural field is homogeneous and isotropic, the weight function is identical for all neurons and depends only on the distance between interacting neurons. The model thus is simplified but is still able to capture the essential properties of a neural system. For the firing rate function $f(x)$, we use the following half-sigmoidal function (Termsaithong et al. 2012)

$$f(x) = \frac{2}{1 + e^{-ax\Theta(x)}} - 1, \quad (3)$$

where $\Theta(x)$ is a Heaviside step function. The negative input cannot send out any output. Here, a is a parameter that controls the steepness of the function.

The firing rate function we used in (3) is not quite common. We used it because it can feature the second-order phase transition. However, it should be noted that similar firing rate functions are used (Kishimoto and Amari 1979; Benayoun et al. 2010).

Next, we add a noise source $u(x, t)\xi(x, t)$ and a small constant external field $h(x) = h$, which represents background

activity, to Eq. (1), and the model can display noisy spontaneous activity. Now, we have a neural field model (Termsaithong et al. 2012) that describes spontaneous activity of the brain as follows:

$$\frac{1}{\alpha} \frac{\partial u(x, t)}{\partial t} = -u(x, t) + \int_{-L}^L w(x-y)f(u(y, t))dy + h + u(x, t)\xi(x, t). \quad (4)$$

Here, ξ is a white Gaussian noise with zero mean and $\langle \xi(x, t)\xi(x', t') \rangle = \sigma^2 \delta(x-x')\delta(t-t')$. σ^2 is the noise intensity. The integration domain $(-\infty, \infty)$ is replaced by $[-L, L]$ for a finite system. The multiplicative noise guarantees an absorbing state, or a uniform stationary solution $u(x) = 0$ for all x , and preserves the phase transition when the noise is introduced into the system. We will show next that a critical point stays in the transition between absorbing and non-absorbing states.

Critical point

The neural field model of Eq. (1) that contains the weight and firing rate functions shown by Eqs. (2) and (3), respectively, features second-order phase transition and a critical point. A steepness variable a in Eq. (3) serves as a control parameter. To identify a critical point, we need to determine at which value of the parameter a , a uniform stationary solution $u(x) = 0 = u_0$ begins to become unstable, or a small perturbation in u_0 will grow over time. We have achieved this by considering the bifurcation diagram of an order parameter $\langle u \rangle = \frac{1}{2L} \int_{-L}^L u(x)dx$ (Termsaithong et al. 2012) versus a control parameter a where the size of L is a half of the field (Fig. 1). According to the diagram, many possible stationary neural activity patterns (bump patterns) can be obtained. However, the point at which a nonzero stationary solution and the order parameter $\langle u \rangle$ begin to emerge is $a_c \approx 1.782$, which is the position of second-order phase transition, i.e., a critical point (Termsaithong et al. 2012). In the control parameter space, we define the left side of the critical point ($a < a_c$) as a subcritical region and the right side of the critical point ($a > a_c$) as a supercritical region.

We performed neural field simulations in a one-dimensional lattice with a lattice size $\Delta x = 0.5$. The activity at point x represents the total activity of neural populations in the range $[x - \frac{\Delta x}{2}, x + \frac{\Delta x}{2}]$. The parameter value $a = 1.782$ accounts for the critical region. We use $L = 20$ and apply a periodic boundary condition $u(-L, t) = u(L, t)$ to reduce a finite-size effect. The initial condition is $u(x) = 0$ for all x , while the other parameters, namely, decay rate $\alpha = 0.2$, noise intensity $\sigma = 1$, and background activity $h = 0.0001$.

Fig. 1 Bifurcation diagram of the neural field model. The blue, red, green, pink, and turquoise lines represent patterns with 1, 2, 3, 4 bumps, and no bump, respectively. (Color figure online)

Probability distribution of cluster sizes

We also determine a probability distribution of cluster sizes of high activity from each region. Here, we use $a = 1.582$, 1.782, and 1.982 to represent subcritical, critical, and supercritical regions, respectively. To study the probability distribution of cluster sizes, we omit time series from $t = 0$ to $t = 1,000$, wherein the neural activity does not yet reach its stationary state, from the simulation samples. Furthermore, since the averaged activity levels differ substantially for different regions, we do not compare them directly. Instead, we transform the activity in each sample of all regions to its corresponding z-scores. Then, we define a cluster by a sequence of points whose z-scores are higher than two in consecutive time steps, and the cluster terminates when there is no such point in the next time step. The cluster size is defined by the total number of points in the cluster.

Dynamical correlation measure

From the neural activity simulations, we compute the Pearson correlation of temporal activity between each pair of lattice points. Then, we define the time window of width Δt , which is the length of time series used to compute correlation coefficients at each step; in this research, we use $\Delta t = 500, 1,000$, and 2,000. This time window is moved step by step until it covers all the temporal extent. As a result, we obtain a set of correlation matrices, which describe the dynamics of correlation coefficients. Then we can compare the dynamical correlation patterns among subcritical, critical, and supercritical regions.

Dynamical functional network and community structure

Now that we have computed a full correlation matrix for each step in time, we can construct a dynamic weighted undirected network whose nodes are the lattice points of the field and weighted edges are the correlation coefficients between each pair of points. A functional connectivity network of the neural field can be studied through this construction.

There are many methods for network community detection. In this research, we employ the Louvain method (Blondel et al. 2008) which is widely used for this task. This method detects non-overlapping communities, which are simpler to evaluate than overlapping communities. It uses greedy optimization to maximize a benefit function called modularity. Modularity is a quantity used to measure how well a network organizes itself into communities or modules.

Modularity values range from 0 to 1. A high modularity suggests good community structure, which means dense connections among nodes inside the same modules and thinner connections among nodes of different modules. In fact, modularity is the difference between the actual fraction of edges/weights in a given community and the expected fraction found in a random network. Generally, there are many forms of modularity. For a network of n nodes and m edges with an adjacency matrix A whose element A_{ij} contains the number of edges between nodes i and j , the most common form of modularity is defined (Newman 2006) as

$$Q = \frac{1}{2m} \sum_{ij} \left(A_{ij} - \frac{k_i k_j}{2m} \right) \delta(g_i, g_j), \quad (5)$$

where k_i is the degree of node i , and g_i is the community to which node i is assigned. $\delta(g_i, g_j)$ is the Kronecker delta, where $\delta(g_i, g_j) = 1$ if $g_i = g_j$ and 0 otherwise. $\frac{k_i k_j}{2m}$ is the expected number of edges connecting nodes i and j in the random network, and then, summation over all pairs of nodes in the same communities is carried out. The definition of modularity in (5) is for unweighted networks, also called binary networks, which means the weight of each edge is either 1 (edge exists) or 0 (no edge). When this definition is applied to weighted networks whose edge weights can be any real number, such as our dynamical functional connectivity, some definitions require modifications. For a weighted network, the adjacency matrix A contains weights between each pair of nodes. k_i becomes the strength of node i , i.e., $k_i = \sum_j A_{ij}$, and $m = \frac{1}{2} \sum_{ij} A_{ij}$.

Here, we use the asymmetric measure of modularity in networks with positive and negative weights proposed by Rubinov and Sporns (2011) and their freely available algorithmic MATLAB code to calculate modularity and

detect communities. This modularity is generalized for networks that have both positive and negative weights. Herein the positive weights in the same communities are maximized, while the negative weights among different communities are minimized. The variables in Eq. (5) are modified to be classified into two types, corresponding to positive and negative weights. A^+ is the adjacency matrix for positive edges. If the connection weight between nodes i and j is negative, then $A_{ij}^+ = 0$. In the same way, A^- is the adjacency matrix for negative edges. If the connection weight between nodes i and j is positive, then $A_{ij}^- = 0$. The two modularities are defined as

$$Q^+ = \frac{1}{2m^+} \sum_{ij} \left(A_{ij}^+ - \frac{k_i^+ k_j^+}{2m^+} \right) \delta(g_i, g_j), \quad (6)$$

$$Q^- = -\frac{1}{2m^-} \sum_{ij} \left(A_{ij}^- - \frac{k_i^- k_j^-}{2m^-} \right) \delta(g_i, g_j), \quad (7)$$

where $k_i^\pm = \sum_j A_{ij}^\pm$ and $m^\pm = \frac{1}{2} \sum_{ij} A_{ij}^\pm$. However, Rubinov and Sporns (2011) argued that in functional brain networks, positive and negative weights do not hold the same importance. Therefore, the quantity to be maximized is not as simple as $Q = Q^+ + Q^-$ but is instead

$$\begin{aligned} Q &= Q^+ + \frac{m^-}{m^+ + m^-} Q^- \\ &= \frac{1}{2m^+} \sum_{ij} \left(A_{ij}^+ - \frac{k_i^+ k_j^+}{2m^+} \right) \delta(g_i, g_j) \\ &\quad - \frac{1}{2(m^+ + m^-)} \sum_{ij} \left(A_{ij}^- - \frac{k_i^- k_j^-}{2m^-} \right) \delta(g_i, g_j). \end{aligned} \quad (8)$$

Q^- is weighted by $\frac{m^-}{m^+ + m^-}$ because the contribution of negative weights to the community structure is less than the contribution of positive ones.

As stated in the previous section, the interval $t \in [0, 1,000]$ of the time series is omitted from the samples. We also measure a number of modules for each step in time. Moreover, to investigate temporal variations in the community structure, we measure the variation of information (Fenn et al. 2009) between the community configuration at the previous time step C_1 and that at the current time step C_2 as follows:

$$\hat{V}(C_1, C_2) = \frac{S(C_1) + S(C_2) - 2I(C_1, C_2)}{\log n}, \quad (9)$$

where n is the total number of nodes in the network, and S is the entropy of a given community configuration defined by

$$S(C) = -\sum_{k=1}^K P(k) \log P(k). \quad (10)$$

Here, k is the community index, and K is the number of communities in the network. $P(k)$ is the probability that an arbitrary node will belong to community k . Suppose that community k consists of n_k nodes, so $P(k) = \frac{n_k}{n}$. Function I in Eq. (9) is the mutual information between configurations C_1 and C_2 , which is defined by

$$I(C_1, C_2) = \sum_{k_1=1}^{K_1} \sum_{k_2=1}^{K_2} P(k_1, k_2) \log \frac{P(k_1, k_2)}{P(k_1)P(k_2)}, \quad (11)$$

where $P(k_1, k_2) = \frac{n_{k_1 \cap k_2}}{n}$, and $n_{k_1 \cap k_2}$ is the number of nodes that belong to both communities k_1 and k_2 . Factor $\log n$ in Eq. (9) is used to normalize $\hat{V}$. The variation of information $\hat{V}(C_1, C_2)$ measures the difference between the community configurations C_1 and C_2 . Here, we use it to determine an amount of change of community structure in time. The value of $\hat{V}$ is confined to the interval $[0, 1]$. $\hat{V}(C_1, C_2) = 0$ means that the community configurations C_1 and C_2 are exactly the same, while $\hat{V}(C_1, C_2) = 1$ means that either C_1 or C_2 has each of its single nodes as a single community and the other has only one community consisting of all nodes (Fenn et al. 2009).

The variation of information (9) is also used to measure the variability of community structure across scales. We define this variability by the averaged degree of difference between the community configuration at a given temporal scale and that determined from the entire length of the time series of neural activity, which represents a static functional connectivity network. High variability means that the dynamical community structure at a given scale and the static one are somewhat unrelated, while low variability implies that they are quite similar.

Other than $b = 1$ of the weight function (2), which is mainly used in this research, we also examine the community structure of neural activity in a field with slight variation in parameter b , particularly values of $b < 1$. The parameters c and d are fixed as in the original case. The value of b has an influence on the inhibition degree of the weight function. A small b causes stronger and wider inhibitory connection, as shown in Fig. 2.

Results

Pattern formation and probability distribution of cluster sizes

Figure 3 shows spatio-temporal patterns of neural activity in Eq. (4) for different values of parameter a that cover subcritical, critical, and supercritical regions with the same noise realization. Note that intermittent activity patterns can appear only in the critical region. These intermittent patterns are analogous to neuronal avalanches in cortex

Fig. 2 Weight function (2) with three different values of parameter b

tissues. In subcritical regions, patterns are the absorbing state perturbed by noise, while the system shows Turing patterns (strips in Fig. 3c) in the supercritical region at $a = 1.982$. However, when a increases further, the Turing pattern is gradually destabilized with mergence (Fig. 3e), and the pattern finally converts into a homogeneous pattern perturbed by noise as in a subcritical region. Note that the emerging Turing patterns appear as wandering bumps, whose positions can slightly deviate from their positions in the previous time step. The pattern in the critical region also exhibits wandering bumps, although the bumps display avalanche-like behavior (Fig. 3b).

We further measure the probability distribution of cluster sizes and find that the distribution in the critical region only exhibits power-law behavior. The exponent of this power-law distribution is approximately -1.5 (see Fig. 4). Away from the criticality, although the probability distributions are partly straight lines in a log-log plot with exponents more than -1.5 (less steep than the distribution in the critical region), their tails do not obey the power law. As a result, a very small cluster has a higher probability, but a cluster of intermediate size has a lower probability at criticality. Furthermore, a very large cluster is found in the critical region only as shown in Fig. 4.

Dynamical correlation and community structure

The time evolution of correlation coefficients is considered using a moving time window, as shown in Fig. 5, which displays only correlation coefficients between point $x = 0$ and all other points (seed-based correlation with $x = 0$ as a seed) for various temporal scales. $a = 1.582$, 1.782 , and 1.982 correspond to subcritical, critical, and supercritical regions, respectively. The correlation coefficient at time t represents the correlation between the time series in the time window of range $[t - \Delta t, t]$. We observe that at the critical point, the dynamical correlation is higher than in

Fig. 3 Spatio-temporal patterns of neural activity at various values of parameter a . The color scales represent levels of neural activity. **a** ($a = 1.582$) and **d** ($a = 1.382$) are in the subcritical region.

b ($a = 1.782$) is in the critical region. **c** ($a = 1.982$) and **e** ($a = 2.182$) are in the supercritical region

Fig. 4 Probability distribution of cluster sizes in subcritical, critical, and supercritical regions. The black dashed line is the power-law distribution with the exact exponent of -1.5

other regions. Furthermore, spatio-temporal clusters of highly correlated and anticorrelated lattice points are found to be outstanding in the critical region. Interestingly, there is switching between high correlation and anticorrelation along the time axis, which is sharper in the critical region. Both characteristics of the outstanding spatio-temporal correlation clusters and sharper switching are also robust across temporal scales.

Each data point in Fig. 6 shows averaged values over 20 simulation samples of the time-averaged modularity Q in Eq. (8), the number of modules, and the variation of information in Eq. (9), respectively, for three different temporal scales. Note that the same set of noise realizations is used to simulate the neural activity samples for each value of parameter a . For the short temporal scales ($\Delta t = 500$ and $\Delta t = 1,000$), it appears that the dynamical networks are most well-organized into communities in exactly the critical region because the time-averaged Q is greatest. On the other hand, the time-averaged numbers of modules and variation of information are lowest in the critical region. The smallest time-averaged variation of information in the critical region indicates that the community structure here changes temporally with the smallest degree, and hence it is most stable. However, for a long temporal scale ($\Delta t = 2,000$), these optimum values shift slightly into the supercritical region. For all three quantities at all the scales around the critical point, the variation in their values in the subcritical direction is sharper than that in the other direction.

When considering the variability, the result in Fig. 7 shows that it takes high values when away from criticality and then decreases until it reaches its lowest value at $a = 1.982$, which is in the supercritical region but not far from the critical point, for all temporal scales. There is large change in variability at point $a = 1.682$ and $a = 2.182$. While parameter a keeps increasing from the

Fig. 5 Dynamical correlation patterns of neural activity in the Fig. 3a–c. The first, second, and third rows represent $\Delta t = 500$, $\Delta t = 1,000$, and $\Delta t = 2,000$, respectively

leftmost point in Fig. 7, the variability keeps decreasing until it reaches its lowest value. However, an interesting point is that the decreasing trend is disrupted when the system passes through the critical point, where the variability increases slightly. In addition, at each value of parameter a , the variability in the longer temporal scale is lower than that in the shorter scale.

Next, we determine the dynamical community structure at scale $\Delta t = 500$ when parameter b of the weight function (2) is changed to 0.5. The shape of this weight function makes greater and wider influence of inhibitory connectivity than our original one, as shown in Fig. 2. In this case, a critical point is approximately at $a = 1.499$. The results are shown in Fig. 8. Interestingly, the result of the time-averaged Q is the opposite of that in the original case. The averaged modularity is lowest at the critical point. However, the lowest averaged variation of information remains in the critical region. There is a drop in the averaged number of modules at the critical point, but it is not an optimal point. On the other hand, if we consider Q^- in Eq. (7), which is independent of the size of positive correlation cluster in the correlation matrix, instead of Q , the

results will not qualitatively change from the original $b = 1$ case; the greatest modularity, the lowest number of modules and the lowest variation of information are obtained at the critical point as shown in Fig. 9.

Moreover, we found that when the value of parameter b or an amount of inhibitory connection is varied, an averaged ratio between numbers of lattice points displaying positive and negative correlation at the corresponding critical point varies as well. Figure 10 shows this ratio at different values of b . The averaged ratio is closest to 1 and lowest at $b = 1$, which is our original weight function. Away from $b = 1$, the ratio continues to increase, although it rises much sharply along the left side (increasing inhibition) than the right side (decreasing inhibition). Note that even if at $b = 1.25$, the ratio is also near 1, and its value at each time step spreads widely around the average considering the combining standard deviation over all time steps of 20 simulation samples. The formation of a large positive correlation cluster in a correlation matrix at each time step causes an asymmetry between the numbers of points showing the positive and negative correlations, and hence, the ratio deviates from 1.

Fig. 6 Community structure of neural activity at various values of a . The data represent averaged values over 20 simulated samples, while the *error bars* represent averaged standard deviations.

a Modularity Q , **b** the number of modules, and **c** variation of information

Fig. 7 Variability as a function of parameter a across three temporal scales. The data represent averaged variability over 20 simulated samples, while the *error bars* represent averaged standard deviation. The *dotted line* indicates position of the critical point. The *dashed lines* indicate the points where data largely change, namely at $a = 1.682$ and $a = 2.182$, respectively

Discussion

Effect of noise to a critical point

In our model, in fact, the multiplicative noise shifts the critical point. However, the shifted value is very small, so

we comparatively use the critical point of the system with no noise, which is much more convenient to determine. This effect of multiplicative noise that induces stability of the absorbing state in the supercritical region was found in other dynamical systems too.

For the dynamical systems with bifurcations, the additive noise, when introduced to systems, does not have any effect on positions of bifurcation points, but if the multiplicative noise is presented, a so-called noise-amplitude-dependent postponement can be induced (Mackey et al. 1990). It is a shift of a value of control parameter where bifurcation occurs, which is the same phenomenon we found in our model. However, the position of bifurcation point does not lastingly keep shifting when noise keeps increasing. If the noise intensity is sufficiently high, the order parameter will become disordered burst-like activity. This is a kind of order-disorder transition (Klemm et al. 2003).

Pattern formation in a neural field

The spatially periodic patterns as observed in a particular interval of the neural field's parameter a (a part of supercritical region) are commonly formed when a weight function with both excitation and inhibition is applied (Ermentrout and Cowan 1979; Tass 1995), even if the stationary patterns become wandering bumps when multiplicative noise is introduced. A similar wandering bump

Fig. 8 Community structure of a neural field with the modified weight function ($b = 0.5$). The data represent averaged values over 20 simulated samples, while the *error bars* represent averaged

standard deviations. The *dotted line* indicates the position of the critical point. **a** Modularity Q , **b** the number of modules, and **c** the variation of information

Fig. 9 The same as Fig. 8 but Q^- is used to determine the community structure instead of Q

Fig. 10 Ratio of the area of positive correlation to that of negative correlation at the corresponding critical point as parameter b varies. Parameters c and d are fixed at 1 and $1/2$, respectively. The data are averaged ratios over 20 simulated samples. The *error bars* are combining standard deviations over all time steps and all samples

pattern is also found in a stochastic neural field with additive noise (Tass 1995) and a deterministic spiking neural network model with fast synaptic interaction (Chow

and Coombes 2006); Amari's model used in our research is equivalent to a slow synaptic version of the model in Chow and Coombes (2006). Both studies demonstrated that the wandering bumps correspond to a diffusion process. However, we did not determine this property in our research. In addition, note that for the simulations shown in Fig. 10 with various values of b , there is no Turing pattern emerging for b whose value is considerably higher than 1 because its inhibitory connections are relatively small compared to the excitatory connections.

The intermittent neural activity of our simulations in the critical region (Fig. 3b) resembles neuronal avalanches. Although the bump pattern was not discovered in the empirical experiment on neuronal avalanches by Beggs and Plenz (2003), some spontaneous cortical activity was observed to be localized, intermittent, and wandering (Petersen et al. 2003; Han et al. 2008), which is similar to our result of the neural activity pattern in Fig. 3b.

In the supercritical region not far from the critical point (Fig. 3c), neural activity can only occur as noise-perturbed spatially periodic states, which occupied the entire field. Nevertheless, at criticality, neural activity can occur transiently in a state of any combinations of bump numbers

allowed by the size of the field and the connectivity trait. Then, it moves to another state. This implies that at a critical point, a neural field possesses a relatively great number of metastable states, and the system is able to itinerate over different available states. On the contrary, the state of pattern in the supercritical region rarely, if ever, performs state switching.

Other than the simple spatially periodic patterns observed from our simulations, with the various options of weight function $w(x)$, firing rate function $f(x)$, and possibly additional terms assigned to a field, many kinds of patterns have been observed, such as a traveling wave (Wilson and Cowan 1973), localized bump (Amari 1977), and spiral wave (Laing 2005) and breather (Folias and Bressloff 2004) in two-dimensional systems. There is a possibility that we can find critical points of the neural field models that induce these patterns.

Critical exponent of cluster sizes

When the probability distribution of cluster sizes in our simulations is considered, it appears that at criticality, the probability distribution features power-law behavior with the critical exponent of -1.5 , which coincides with that of neuronal avalanches (Beggs and Plenz 2003). The intermittency and the exponent of -1.5 emerge if and only if our neural field is in the critical region, as shown in Figs. 3 and 4. Moreover, Beggs and Plenz (2003) also demonstrated that the propagation of neuronal avalanche activity can be described by a critical branching process, which produces the same value of the critical exponent. This may be a result of the universality of critical phenomena. However, at this stage, we have not yet been able to conclude whether our model is in the same universality class of the critical branching process. Further, note that the issue of neuronal avalanches being genuinely critical is still controversial (for examples, see Benayoun et al. 2010; Touboul and Destexhe 2010; Plenz and Chialvo 2009; Klaus et al. 2011).

Dynamical correlation patterns

The correlation degree is highest at the critical region, as expected. Interestingly, another phenomenon found to be very prominent in the critical region is the correlation switching between high correlation and anticorrelation, which robustly occurs across different temporal scales. This kind of switching was also found in the fast neural activity of simulations based on the macaque cortex's anatomical connections (Honey et al. 2007).

In our model, correlation switching stems from the high correlation together with the long correlation length in the critical region. The long correlation length allows distant

points to interact strongly and avalanches to travel further away from their original positions. The traveling of avalanches including smaller localized activity causes shifting between positive and negative activity patterns at a given spatial point. As a result, correlation switching occurs. Our hypothesis is that this phenomenon can occur in any system with propagating avalanches driven constantly by an external stimulus, such as a sandpile constantly driven by additional sand grains.

Furthermore, this switching along with Hebbian learning (Hebb 1949) or other kinds of plasticity can probably improve the learning performance of the brain because it provides various interaction patterns, both correlated and anticorrelated, to be flexibly explored by the neural system. It was found that a neural network model that can generate avalanches in spontaneous activity can learn complex rules, such as XOR and the three-input random rule (de Arcangelis and Herrmann 2010). This is also consistent with the work of Tanaka et al. (2009). They proposed a learning algorithm that maximizes information in recurrent neural networks, and found that when external input is absent, the network exhibits neuronal avalanche activity.

Community structure

Community detection used in this research is related to modularity maximization. The disadvantage of this method is the degeneracy of high modularity values. It means that the optimization algorithm can reach the same maximized modularity but a different network configuration is obtained. However, this drawback is compensated by averaging the relevant quantities over thousands of largely overlapped consecutive time windows. Moreover, degeneracy can possibly be an intrinsic property of functional brain networks and not just a methodological problem (Rubinov and Sporns 2011).

For the community structure of a functional connectivity network at short temporal scales ($\Delta t = 500$ and $\Delta t = 1,000$), at criticality, large modularity indicates that the neural field splits into different modules or is functionally well segregated (Schwarz et al. 2008; Bassett et al. 2011), and a small number of modules indicates that the neural activity is functionally well integrated (Bassett et al. 2011). These results agree with the fact that the brain has to perform both integrated and distributed functions (Chialvo et al. 2008; Sporns et al. 2000; Tononi et al. 1994), and we numerically show that the community structure at criticality is most appropriate to perform both functions at least for short time scales. Regarding the variation of information, we also show that at criticality, the community of a functional connectivity network minimally reorganizes itself in time. This is further reflected in outstanding spatio-temporal clusters of correlation and anticorrelation in the

middle column of Fig. 5. Lewis et al. (2009) found that performance of visual perceptual learning is better when a functional network changes only slightly after learning. Another study by de Arcangelis and Herrmann (2010) reported that a neural network can obtain higher probability of success if the plastic adaptation is slower. It is possible that stability of functional connectivity contributes to learning enhancement. Asymmetry around the critical point is caused by emerging spatial patterns in the supercritical region. If there is no emerging pattern, for example, when a weight function of pure excitation is used, the results will be symmetric.

The slight shift of optimal points to the supercritical region in the long temporal scale ($\Delta t = 2,000$) is induced by strip patterns (Fig. 3c). At the temporally large scale, the regularity of the pattern becomes dominant over a faster fluctuation and gives rise to regularity in a correlation matrix, which is in turn able to improve the community structure. However, the trade-off of this slight improvement is the loss of flexibility. Furthermore, spatial pattern formation similar to what we found (but in two-dimensional systems) has been hypothesized to be a source of some types of visual hallucination (Ermentrout and Cowan 1979; Tass 1995) and not found in the brain spontaneous activity of healthy subjects.

As brain operation is performed by interrelated processes over multiple temporal scales (Ulanovsky et al. 2004; Honey et al. 2007; La Camera et al. 2006), the degree of similarity or the variability of a functional network's community structure among various scales may be relevant. From Fig. 7, the lowest value of the variability is at $a = 1.982$ where the spatial pattern is most pronounced, and this is true for all three scales. This result implies that the regularity of spatially periodic patterns can restrain the flexibility of the community structure. As a result, the more pronounced the pattern is, the less is the difference between the community structures of different scales. This also results in large change of variability at point $a = 1.682$ and $a = 2.182$; the value of a in an interval $[1.682, 2.182]$ is where the spatial patterns can arise, while outside of it, the neural activity is rather dominated by noise. In the regions dominated by noise, high variability indicates that the community structure in each scale is somewhat unrelated, and it probably did not gain much benefit for information processing across multiple time scales. Ignoring such regions and considering regions where $a \in [1.622, 2.182]$, it appears that at the critical point, the variability is high, but is less than that at the supercritical region of $a = 2.182$ where the spatial pattern almost disappears (Fig. 3e). Hence, the variability in the critical region is a mediator between high regularity and disorder.

The reverse result of Q when the modified weight function with $b = 0.5$ is used (Fig. 8a) is caused by the

formation of a large positive correlation cluster in a correlation matrix. The smaller than 1 the parameter b is, the larger is the positive correlation cluster in each time window (the result is not shown but can be implied from Fig. 10). In our model, at criticality, a negative activity area in the field tends to correlate with the other negative activity areas, and a positive activity area tends to correlate with the other positive activity areas. This leads to the formation of positive correlation clusters in a correlation matrix and modules in the community structure. Therefore, the decrease of parameter b with wider inhibitory connectivity and hence wider negative activity areas evokes few large modules, while the module size of positive activity becomes smaller. In this case, it is not the poor quality of community partition but the asymmetry in module size that gives the lowest Q in the critical region. That is why, the result of Q^- , which is independent of module size, remains consistent with the model with original weight function ($b = 1$). The asymmetry in module size leads to an increase in the term $\frac{k_i^+ k_j^+}{2m^+}$ in Eq. (6). Consequently, Q^+ decreases and hence Q .

However, it was found that the ratio of the area of positive correlation to that of negative correlation in brain spontaneous activity is close to 1 in healthy subjects, while it is much higher in patients who suffer from chronic pain (Baliki et al. 2008). From Fig. 10, it appears that our original parameter value $b = 1$ is the most appropriate value of the weight function (2) (for $c = 1$ and $d = 1/2$) to study dynamical correlation patterns and community structure of spontaneous activity.

In summary, we used a neural field model tuned to a critical point and studied its dynamical correlation patterns and corresponding community structure of dynamical functional connectivity in comparison with other regions, namely, the subcritical and supercritical regions. In the critical region, we found many characteristics that may support information processing of the brain. First, high correlation degrees and correlation switching might uphold a learning process. Second, the high modularity and a low number of modules imply efficient functional segregation and integration, respectively, which are both necessary for brain functions. Third, the high stability of dynamical functional connectivity may be involved in good performance of learning. Finally, the variability or flexibility of community structure across multiple time scales can be a mediator between regulated and disordered configurations.

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