I. OVERVIEW

We first give a brief summary of the mathematical foundations of Lyapunov spectra (II) and our concrete implementation for rate networks (III). We give and introduction to Kolmogorov-Sinai entropy rate and Kaplan Yorke attractor dimensionality (IV). We extend the approach to random dynamical systems and discuss the implementation of Lyapunov spectra for non-autonomous networks with time-dependent input (V). Then we give details about the PCA-based dimensionality estimate (VI).

II. LYAPUNOV SPECTRUM OF A DYNAMICAL SYSTEM

An autonomous dynamical system is usually defined by a set of ordinary differential equations $\mathrm{d}\mathbf{x}/\mathrm{d}t = \mathbf{F}(\mathbf{x}),\ \mathbf{x} \in \mathbb{R}^N$ in the case of continuous-time dynamics, or as a map $\mathbf{x}_{s+1} = \mathbf{f}(\mathbf{x}_s)$ in the case of discrete-time dynamics. In the following, the theory is presented for discrete-time dynamical systems for ease of notation, but everything directly extends to continuous-time systems [160]. In our specific case, we study the discrete network dynamics for small Δt. This corresponds to the usual Euler method in the autonomous case or to the Euler-Maruyama method [161] in the non-autonomous case with stochastic input drive. We confirm our autonomous results for small Δt using the Tsitouras 5/4 Runge-Kutta method, the Dormand-Prince 5/4 Runge-Kutta method, the Bogacki-Shampine 5/4 Runge-Kutta method, and Verner's 9/8 Runge-Kutta method [162–165] employing the implementation provided by the DifferentialEquations.jl package in the programming language Julia [166, 167]. Together with an initial condition $\mathbf{x}_0$, the map forms a trajectory. As a natural extension of linear stability analysis, one can ask how an infinitesimal perturbation $\mathbf{x}_0' = \mathbf{x}_0 + \epsilon\mathbf{u}_0$ evolves in time. Chaotic systems are sensitive to initial conditions; almost all infinitesimal perturbations $\epsilon\mathbf{u}_0$ of the initial condition grow exponentially with time $|\epsilon\mathbf{u}_t| \approx \exp(\lambda_{\max} t)|\epsilon\mathbf{u}_0|$. Finite-size perturbations, therefore, may lead to a drastically different subsequent behavior. The largest Lyapunov exponent $\lambda_{\max}$ measures the average rate of exponential divergence or convergence of nearby initial conditions:

$$\lambda_{\max}(\mathbf{x}_0) = \lim_{t\to\infty} \frac{1}{t} \lim_{\epsilon\to 0} \log \frac{||\epsilon\mathbf{u}_t||}{||\epsilon\mathbf{u}_0||} \tag{1}$$

In dynamical systems that are ergodic on the attractor, the Lyapunov exponents do not depend on the initial conditions, as long as the initial conditions are in the basins of attraction of the attractor. Note that it is crucial to first take the limit $\epsilon \to 0$ and then $t \to \infty$, as $\lambda_{\max}(\mathbf{x}_0)$ would be trivially zero for a bounded attractor if the limits are exchanged, as $\lim_{t\to\infty} \log \frac{||\epsilon\mathbf{u}_t||}{||\epsilon\mathbf{u}_0||}$ is bounded for finite perturbations even if the system is chaotic. To measure m Lyapunov exponents, one has to study the evolution of m independent infinitesimal perturbations $\mathbf{u}_s$ spanning the tangent space:

$$\mathbf{u}_{s+1} = \mathbf{D}_s\mathbf{u}_s \tag{2}$$

where the $N \times N$ Jacobian $\mathbf{D}_s(\mathbf{x_s}) = \mathrm{d}\mathbf{f}(\mathbf{x_s})/\mathrm{d}\mathbf{x}$ characterizes the evolution of generic infinitesimal perturbations during one step. Note that this Jacobian along the trajectory is equivalent to a stability matrix only at a fixed point, i.e., when $\mathbf{x}_{s+1} = \mathbf{f}(\mathbf{x}_s) = \mathbf{x}_s$.

We are interested in the asymptotic behavior, and therefore we study the long-term Jacobian

$$\mathbf{T}_t(\mathbf{x}_0) = \mathbf{D}_{t-1}(\mathbf{x}_{t-1}) \dots \mathbf{D}_1(\mathbf{x}_1)\mathbf{D}_0(\mathbf{x}_0). \tag{3}$$

Note that $\mathbf{T}_t(\mathbf{x}_0)$ is a product of generally noncommuting matrices. The Lyapunov exponents $\lambda_{\max} \geq \lambda_2 \cdots \geq \lambda_N$ are defined as the logarithms of the eigenvalues of the Oseledets matrix

$$\mathbf{\Lambda}(\mathbf{x}_0) = \lim_{t\to\infty} [\mathbf{T}_t(\mathbf{x}_0)^\top \mathbf{T}_t(\mathbf{x}_0)]^{\frac{1}{2t}}, \tag{4}$$

where $\top$ denotes the transpose operation. The expression inside the brackets is the Gram matrix of the long-term Jacobian $\mathbf{T}_t(\mathbf{x}_0)$. Geometrically, the determinant of the Gram matrix is the squared volume of the parallelotope spanned by the columns of $\mathbf{T_t}(\mathbf{x_0})$. Thus, the exponential volume growth rate is given by the sum of the logarithms of its first m (sorted) eigenvalues. Oseledets' multiplicative ergodic theorem guarantees the existence of the Oseledets matrix $\mathbf{\Lambda}(\mathbf{x}_0)$ for almost all initial conditions $\mathbf{x}_0$ [73]. In ergodic systems, the Lyapunov exponents λ_i do not depend on the initial condition $\mathbf{x}_0$. However, for a numerical calculation of the Lyapunov spectrum, Eq. 4 cannot be used directly because the long-term Jacobian $T_t(\mathbf{x}_0)$ quickly becomes ill-conditioned, i.e., the ratio between its largest and smallest singular value diverges exponentially with time.

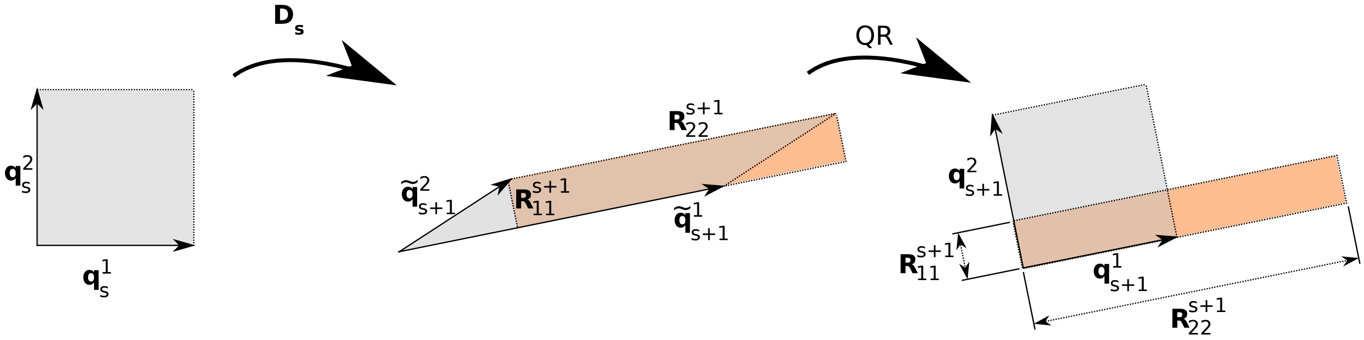

Figure 1. **Geometric illustration of Lyapunov spectrum calculation.** An orthonormal matrix $\mathbf{Q}_s = [\mathbf{q}_s^1, \mathbf{q}_s^2, \dots \mathbf{q}_s^m]$, whose columns are the axes of an m-dimensional cube, is rotated and distorted by the Jacobian $\mathbf{D}_s$ into an m-dimensional parallelotope $\widetilde{\mathbf{Q}}_{s+1} = \mathbf{D}_s\mathbf{Q}_s$ embedded in $\mathbb{R}^{\mathbf{N}}$. The figure illustrates this for $m = 2$, in which case the columns of $\widetilde{\mathbf{Q}}_{s+1}$ span a parallelogram, which can be divided into a right triangle and a trapezoid and rearranged into a rectangle. Thus, the area of the gray parallelogram is the same as that of the orange rectangle. The QR-decomposition reorthonormalizes $\widetilde{\mathbf{Q}}_{s+1}$ by decomposing it into the product of an orthonormal matrix $\mathbf{Q}_{s+1} = [\mathbf{q}_{s+1}^1, \mathbf{q}_{s+1}^2, \dots \mathbf{q}_{s+1}^m]$ and the upper-triangular matrix $\mathbf{R}^{s+1}$. $\mathbf{Q}_{s+1}$ describes the rotation of $\mathbf{Q}_s$ caused by $\mathbf{D}_s$. The diagonal entries of $\mathbf{R}^{s+1}$ gives the stretching/shrinking along the columns of $\mathbf{Q}_{s+1}$, thus the volume of the parallelotope formed by the first m columns of $\widetilde{\mathbf{Q}}_{s+1}$ is given by $V_m = \prod_{i=1}^m \mathbf{R}_{ii}^{s+1}$. The time-averaged logarithms of the diagonal elements of $\mathbf{R}^s$ give the Lyapunov spectrum: $\lambda_i = \lim_{t_{\text{sim}}\to\infty} \frac{1}{t_{\text{sim}}} \log \prod_{s=1}^t \mathbf{R}_{ii}^s = \lim_{t_{\text{sim}}\to\infty} \frac{1}{t} \sum_{s=1}^t \log \mathbf{R}_{ii}^s$.

III. ALGORITHM FOR CALCULATING LYAPUNOV SPECTRUM OF RATE NETWORKS

For calculating the first m Lyapunov exponents, we exploit the fact that the growth rate of an m-dimensional infinitesimal volume element is given by $\lambda^{(m)} = \sum_{i=1}^m \lambda_i$. Therefore, $\lambda_{\max} = \lambda^{(1)}$, $\lambda_2 = \lambda^{(2)} - \lambda_{\max}$, $\lambda_3 = \lambda^{(3)} - \lambda_{\max} - \lambda_2$, … [60]. The volume growth rates can be obtained via QR-decomposition.

First, we evolve an initially orthonormal system $\mathbf{Q}_s = [\mathbf{q}_s^1, \mathbf{q}_s^2, \dots \mathbf{q}_s^m]$ in the tangent space along the trajectory using the Jacobian $\mathbf{D}_s$:

$$\widetilde{\mathbf{Q}}_{s+1} = \mathbf{D}_s\mathbf{Q}_s \tag{5}$$

To this end, the variational equation $\tau\dot{\mathbf{Q}} = \mathbf{D}(t)\mathbf{Q}$ has to be integrated. A continuous system can be transformed into a discrete system by considering a stroboscopic representation, where the trajectory is only considered at certain discrete time points. We use here the notation of discrete dynamical systems, where this corresponds to performing the product of Jacobians along the trajectory $\widetilde{\mathbf{Q}}_{s+1} = \mathbf{D}_s\mathbf{Q}_s$. We study the discrete network dynamics in the limit of small time step $\Delta t \to 0$ and for discrete time $\Delta t = 1$. The notation can be readily extended to continuous systems [160].

Second, we extract the exponential growth rates using the QR-decomposition,

$$\widetilde{\mathbf{Q}}_{s+1} = \mathbf{Q}_{s+1}\mathbf{R}^{s+1},$$

which uniquely decomposes $\widetilde{\mathbf{Q}}_{s+1}$ into an orthonormal matrix $\mathbf{Q}_{s+1}$ of size $N \times m$ so $\mathbf{Q}_{s+1}^\top\mathbf{Q}_{s+1} = \mathbb{1}_{m\times m}$ and to an upper triangular matrix $\mathbf{R}^{s+1}$ of size $m \times m$ with positive diagonal elements. Geometrically, $\mathbf{Q}_{s+1}$ describes the rotation of $\mathbf{Q}_s$ caused by $\mathbf{D}_s$ and the diagonal entries of $\mathbf{R}^{s+1}$ describe the stretching and shrinking of the columns of $\mathbf{Q}_s$, while the off-diagonal elements represent the shearing. Fig. 1 visualizes $\mathbf{D}_s$ and the QR-decomposition for $m = 2$.

The Lyapunov exponents are given by time-averaged logarithms of the diagonal elements of $\mathbf{R}^s$:

$$\lambda_i = \lim_{t\to\infty} \frac{1}{t} \log \prod_{s=1}^{t} \mathbf{R}_{ii}^s = \lim_{t\to\infty} \frac{1}{t} \sum_{s=1}^{t} \log \mathbf{R}_{ii}^s. \tag{6}$$

Note that the QR-decomposition does not need to be performed at every simulation step, just sufficiently often, i.e., once every s_{ONS} steps such that $\widetilde{\mathbf{Q}}_{s+s_{\text{ONS}}} = \mathbf{D}_{s+s_{\text{ONS}}-1} \cdot \mathbf{D}_{s+s_{\text{ONS}}-2} \dots \mathbf{D}_s \cdot \mathbf{Q}_s$ remains well-conditioned [60]. An appropriate reorthonormalization interval $s_{\mathrm{ONS}} = t_{\mathrm{ONS}}/\Delta t$ thus depends on the condition number, the ratio of the smallest and largest singular value:

$$\kappa_2(\widetilde{\mathbf{Q}}_{s+s_{\mathrm{ONS}}}) = \kappa_2(\mathbf{R}^{s+s_{\mathrm{ONS}}}) = \frac{\sigma_1(\mathbf{R}^{s+s_{\mathrm{ONS}}})}{\sigma_m(\mathbf{R}^{s+s_{\mathrm{ONS}}})} = \frac{\mathbf{R}_{11}^{s+s_{\mathrm{ONS}}}}{\mathbf{R}_{mm}^{s+s_{\mathrm{ONS}}}}. \tag{7}$$

Therefore, the condition number can be estimated based on the ratio of the largest and smallest Lyapunov exponent that is calculated:

$$\kappa_2(\widetilde{\mathbf{Q}}_{s+s_{\mathrm{ONS}}}) \approx \exp\left((\lambda_{\max} - \lambda_m) s_{\mathrm{ONS}} \Delta t\right).$$

Thus, an appropriate reorthonormalization interval is given by $s_{\mathrm{ONS}} = \mathcal{O}\left(\log(\hat{\kappa}_2)/(\lambda_{\max} - \lambda_m)\right)/\Delta t$, where $\hat{\kappa}_2$ is some acceptable condition number. The acceptable condition number depends on the desired accuracy of the entries of $\mathbf{R}^{s+s_{\mathrm{ONS}}}$. An initial transient should be disregarded in the calculation of the Lyapunov spectrum because $\mathbf{h}$ first has to converge towards the attractor and $\mathbf{Q}$ has to converge to the unique eigenvectors of the Oseledets matrix (Eq. 4) [168]. A simple example of this algorithm in pseudocode is:

Jacobian-based algorithm for Lyapunov spectrum

```
initialize h, Q
evolve h until it is on attractor (avoid initial transient)
evolve Q until it converges to the eigenvectors of the backward Oseledets matrix
for s = 1 → s_sim/Δt do
    h ← f(h)
    D ← df/dh
    Q ← D · Q
    if  s ≡ 0 (mod s_ONS) then
        Q, R ← qr(Q)
        γ_i += log(R_ii)
    end if
end for
λ_i = γ_i/t_sim
```

It is guaranteed that under general conditions initially random orthonormal systems will exponentially converge towards a unique basis that is given by the eigenvectors of the Oseledets matrix Eq. 4 [168]. A minimal example of this algorithm in pseudocode is shown in the main text (see III). A feasible strategy to determine the reorthonormalization time interval t_{ONS} is to get first a rough estimate of the Lyapunov spectrum using a short simulation time t_{sim} and a small t_{ONS} and repeat with a longer simulation time and a t_{ONS} based on the Lyapunov spectrum of the rough estimate of the Lyapunov spectrum. Another strategy is, to first iteratively adapt t_{ONS} on a short simulation run to get an acceptable condition number. It should be noted that there exist a diversity of other methods to estimate the Lyapunov spectrum [40, 58, 160, 169].

IV. KOLMOGOROV-SINAI ENTROPY RATE AND KAPLAN YORKE ATTRACTOR DIMENSIONALITY

Entropy rate Chaos of a dynamical system is always associated with a dynamical entropy rate because nearby states, which could not be distinguished by a finite precision readout, are pulled apart by the sensitive dependence on initial conditions [41]. This concept was formalized by Kolmogorov and Sinai in 1959 and termed metric entropy (also called Kolmogorov-Sinai entropy or dynamical entropy rate) [40, 42, 51, 58, 170].

Ruelle showed that the sum of the positive Lyapunov exponents gives an upper bound to the Kolmogorov-Sinai entropy [171]:

$$h_{\mathrm{KS}} \leqslant \sum_{\lambda_i > 0} \lambda_i \tag{8}$$

Equality holds if and only if the system is endowed with an SRB (Sinai-Ruelle-Bowen) measure (Pesin entropy formula) [172]. An f-invariant Borel probability measure μ is an SRB measure if the conditional probability of μ on smooth manifolds is absolutely continuous [173]. f-invariant means here that $\mu\left(f^{-1}(A)\right) = \mu(A)$. The Pesin entropy formula thus says that uncertainty in the prediction of future states comes from positive Lyapunov exponents, or more precisely, from the expanding manifolds with smooth densities [42]. In several classes of dynamical systems, the existence of an SRB measure was proved [174]. The angles between unstable and stable manifolds can be used to test numerically whether a system is hyperbolic. If a dynamical system is hyperbolic, there is always a finite angle between stable and unstable manifolds. In this case, the existence of an SRB measure is guaranteed [51, 175–177].

Attractor dimensionality The trajectory of a dissipative chaotic system with N degrees of freedom does not cover the whole phase space. After a transient period, it relaxes onto an attractor, which has a dimensionality $D \leq N$. This can be a zero-dimensional fixed point, a one-dimensional periodic orbit, a higher-dimensional quasi-periodic orbit, or a strange attractor with typically non-integer dimensionality in the case of a chaotic system. Such a strange attractor is often a fractal set and one classical approach to measuring its dimensionality is box counting. The idea is to count the number M of N-dimensional boxes of side length a that are necessary to cover the attractor. The box-counting dimension is then defined as $D = -\lim_{a\to 0} \frac{\log(M(a))}{\log(a)}$. For increasing dimension, one runs into the curse of dimensionality because the data necessary for the box counting scales exponentially with the dimensionality.

A more generalized concept of dimensionality of fractals is given by the Rényi dimension (also called generalized dimension) [54]. The Rényi dimension of order α is given by

$$D_\alpha = \lim_{\varepsilon\to 0} \frac{1}{\alpha - 1} \frac{\log(\sum_i p_i^\alpha)}{\log \varepsilon} \tag{9}$$

For $\alpha = 0$ the capacity dimension (box-counting dimension) is obtained. $\alpha = 1$ gives the information dimension and $\alpha = 2$ the correlation dimension [52]. Besides box-counting, there exist other sampling-based techniques to obtain entropies and dimensionalities directly from data, e.g., the Grassberger-Procaccia algorithm [52, 53], which estimates the correlation dimension D_2. Similar to the case of box counting, a strict lower bound on the data required to estimate the attractor dimensionality with a fixed desired accuracy scales exponentially in the degrees of freedom D [55, 56]. It is well understood in nonlinear dynamics that such direct approaches of measuring dimensionality are inappropriate for high-dimensional dynamical systems [178].

A more tractable way to quantify the attractor dimension and thus the number of degrees of freedom of a strange chaotic attractor can be obtained based on the Lyapunov spectrum if the equations of motion of the dynamical system are known and differentiable. The attractor dimension is then given by the interpolated number of Lyapunov exponents that sum to zero:

$$D_{\mathrm{KY}} = k + \frac{\sum_{i=1}^{k} \lambda_i}{|\lambda_{k+1}|} \quad \text{with} \quad k = \max_n \left\{ \sum_{i=1}^{n} \lambda_i \geq 0 \right\}. \tag{10}$$

The attractor dimension has been conjectured to be ‘in general’ equivalent to the information dimension D_1 [51, 179–181]. While there exists no proof in general, it has been proven for several low-dimensional systems [182, 183] and for other systems supporting numerical evidence has been found [184]. The following bound on the capacity dimension has been proven: $D_0 \leq D_{KY}$ [182, 185].

Intuitively, the attractor dimension is the dimensionality of the highest dimensional infinitesimal hypersphere, whose volume does not shrink nor grow by the chaotic dynamics. In other words, on the attractor, growth along unstable manifolds is being compensated by shrinking along the stable manifolds, and any D-dimensional hypersphere is merely deformed and the volume is preserved on average.

Remembering the inequalities $h_{\mathrm{KS}} \leq h$ and $D_0 \leq D_{\mathrm{KY}}$, we will call $h = \sum_{\lambda_i>0} \lambda_i$ the entropy rate and $D = D_{\mathrm{KY}}$ the attractor dimension throughout this paper.

V. RANDOM DYNAMICAL SYSTEMS AND TRIAL-TO-TRIAL VARIABILITY

The extension of concepts of the ergodic theory of dynamical systems to input-driven systems was done in the theory of Random Dynamical Systems [186]. This can be useful for neuroscience to better understand trial-to-trial variability, controllability and input-driven chaos (see, e.g., [46, 154]). Consider a stochastic differential equation of the form:

$$\mathrm{d}x_t = a(x_t)\mathrm{d}t + \sum_{i=1}^{N} b_i(x_t) \circ \mathrm{d}W_t^i \tag{11}$$

where $\mathrm{d}W_t^i$ are independent Brownian motions. An associated *stochastic flow map* is a solution for the dynamics, i.e., $F_{t_1,t_2;\zeta}(\mathbf{x}_{t_1}) = \mathbf{x}_{t_2}$ maps the state x from t_1 to t_2, where ζ denotes the realization of the stochasticity. Instead of studying the temporal evolution of some initial measure μ, where each initial condition receives "private" noise, as it is usually done in a Fokker-Planck approach, the theory of random dynamical systems studies the evolution of a *sample measure* μ_ζ^t, defined as

$$\mu_\zeta^t = \lim_{s\to\infty} (F_{-s,\,t;\zeta})_*\mu \tag{12}$$

where the propagator $(F_{-s,\,t;\zeta})_*$ transports the initial measure μ for some fixed white noise realization $\zeta(t)$ defined for all $t \in (-\infty, \infty)$ along the flow $F_{-s,\,t;\zeta}$. In other words, the sample measure μ_ζ^t is the conditional measure at time t given the infinite past history of $\zeta(t)$. Note that in general, while μ_ζ^t depends on both time t and the noise realization ζ, it posses invariant properties, characterizing its structure. For example, the Lyapunov exponents given the input noise realization that we call here conditional Lyapunov exponents $\lambda_{\max} \geqslant \lambda_2 \geqslant \ldots \geqslant \lambda_N$ are independent of the input realization ζ [109].

Two theorems for random dynamical systems link sample measure μ_ζ^t and conditional Lyapunov spectrum in chaotic and stable systems, respectively. First, Ledrappier and Young proved that if $\lambda_{\max} > 0$, then μ_ζ^t is a random SRB (Sinai-Ruelle-Bowen) measure [187]. As a consequence, in contrast to autonomous systems, for random dynamical systems, the Pesin identity $H = \sum\limits_{\lambda_i>0} \lambda_i$ is guaranteed to hold. Note that in contrast to SRB measures of autonomous systems, random SRB measures are time-dependent. However, they have a similar meaning: systems with SRB measure have smooth conditional measures along the unstable manifolds.

In addition, Baxendale and Le Jan showed that if $\lambda_{\max} < 0$ and the stationary measure is ergodic and some nondegeneracy conditions on the measure are fulfilled [110], then μ_ζ^t is a random sink, which means $\mu_\zeta^t(\mathbf{x}) = \delta(\mathbf{x} - \mathbf{x}_t)$, where $\mathbf{x}_t$ is a solution of the stochastic dynamics for a given noise realization ζ [110, 111]. Consequently, any trajectory of a stable rate network driven by white noise will, after finite time, be absorbed into one single trajectory, which is independent of the initial condition but depends only on the noise realization. Equally, any smooth initial measure will asymptotically coalesce into a time-dependent random sink. Note that the theorems by Baxendale and Le Jan do not say when the globally attracting random sink will be reached, which means that for very long transients, its asymptotic existence might have no practical relevance on biologically relevant timescales [42].

VI. PRINCIPAL COMPONENT-BASED DIMENSIONALITY ESTIMATE

We compared the attractor dimension to a principal component-based dimensionality estimate. Principal component analysis (PCA) has been widely used as a dimensionality reduction technique both in experimental and theoretical neuroscience [9, 10, 63–65].

For a given data set, PCA provides the succeeding orthogonal directions that account for most of the variance in the data and the associated fraction of variance explained. Mathematically, PCA is given by the eigenvalue decomposition of the covariance matrix. The number of principal components necessary to account for the majority of the total variance gives an estimate of the number of degrees of freedom of the underlying dynamics. If a few principal components explain most of the variance, the dynamics is mostly constrained to a hyperellipsoid with few long axes. If many principal components are necessary, no such localized structures in the second-order statistics of the collective dynamics are detected. To avoid choosing an arbitrary threshold of variance (e.g., 95 %), one can use a participation ratio, commonly used in physics to quantify, e.g., localization of collective activity modes [188], Anderson localization of waves in a disordered medium [189] or localized Lyapunov vectors [89, 190]. We calculated PCA-based dimensionality estimates both based on the covariance of the total synaptic currents h_i and of the rates $\phi_i = \tanh(h_i)$. For instance, for h_i, we compute the covariance matrix C_{ij}^h:

$$C_{ij}^h = \langle (h_i - \langle h_i \rangle)(h_j - \langle h_j \rangle) \rangle \tag{13}$$

A PCA-based dimensionality estimate is then given by the participation ratio

$$D_{\mathrm{PCA}}^h = \frac{(\sum_{n=1}^N \mu_n^h)^2}{\sum_{n=1}^N \mu_n^{h2}} \tag{14}$$

where μ_n^h is the n^{th} eigenvalue of the covariance matrix C_{ij}^h. If all eigenvalues contribute equally (i.e. $\frac{\mu_n^h}{\sum_i \mu_n^h} = 1/N$), the dimension estimate is $D_{\mathrm{PCA}}^h = N$. Conversely, if only one eigenvalue contributes then $D_{\mathrm{PCA}}^h = 1$ [9, 63, 89].

$D_{\rm PCA}^{\tanh h}$ was calculated the same way, but for the covariance matrix $C^{\tanh h}$ of the firing rates.

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