On the master equation approach to stochastic neurodynamics

Paul C Bressloff

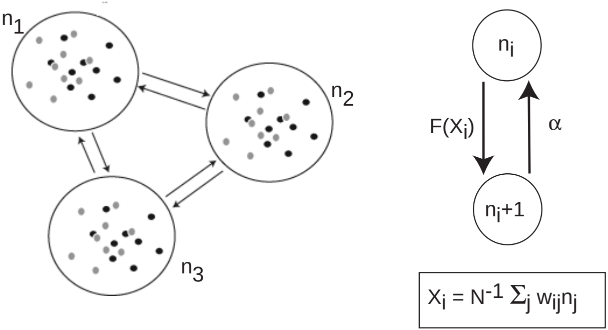
Mathematical Institute and OCCAM, University of Oxford

January 18, 2010

Part I. Master equation

- Consider M homogeneous networks labelled $k = 1, \ldots M$, each containing N identical neurons
- Assume that each neuron can be in one of two states, quiescent or active ie. in the process of generating an action potential.
- Suppose that in the interval $[t, t + \Delta t)$ there are $n_k(t)$ active neurons in the kth population
- Define population activity in terms of the **fraction** of active neurons according to

$$u_k^{(N)}(t) = \frac{n_k(t)}{N}.$$



- Treat the number of active neurons $n_k(t)$ as a stochastic variable that evolves according to a one–step jump Markov process
- Rates of state transitions $n_k \to n_k \pm 1$ are chosen so that in the thermodynamic limit $N \to \infty$ one obtains the deterministic Wilson-Cowan equations – transition rates not unique!

Let $P(\mathbf{n},t)$ with $\mathbf{n}=(n_1,\ldots,n_N)$ denote probability that $m_i(t)=n_i$ for all i

Probability distribution evolves according to birth-death master equation

$$\frac{dP(\mathbf{n},t)}{dt} = \sum_{k=1}^{N}\sum_{r=\pm 1}\left[T_{k,r}(\mathbf{n}_{k,r})P(\mathbf{n}_{k,r},t)-T_{k,r}(\mathbf{n})P(\mathbf{n},t)\right]$$

where $\mathbf{n}_{k,r}=(n_1,\ldots,n_{k-1},n_k-r,n_{k+1},\ldots,n_N)$.

Master equation is supplemented by the boundary conditions $P(\mathbf{n},t)\equiv 0$ if $n_i=N+1$ or $n_i=-1$ for some i.

Transition rates are

$$T_{k,-1}(\mathbf{n})=\alpha \mathbf{n}_k,\quad T_{k,+1}(\mathbf{n})=NF\left(\sum_l w_{kl}n_l/N\right)$$

Multiply both sides of master equation by n_k and sum over all states $\mathbf{n}$. This gives

$$\frac{d}{dt}\langle n_k\rangle = \sum_{r=\pm 1} r\langle T_{k,r}(\mathbf{n})\rangle$$

where $\langle f(\mathbf{n})\rangle = \sum_{\mathbf{n}} P(\mathbf{n},t) f(\mathbf{n})$ for any function of state $f(\mathbf{n})$.

Assume all statistical correlations can be neglected so that $\langle T_{k,r}(\mathbf{n})\rangle \approx T_{k,r}(\langle \mathbf{n}\rangle)$

Setting $u_k = N^{-1}\langle n_k\rangle$ leads to mean–field equation

$$\begin{aligned}\frac{d}{dt}u_k &= N^{-1}[T_{k,+}(N\mathbf{u}) - T_{k,-}(N\mathbf{u})]\\ &= -\alpha u_k + F\left(\sum_l w_{kl}u_l\right) \equiv H_k(\mathbf{u})\end{aligned}$$

1. (Perron–Frobenius theorem): For an irreducible weight matrix $\mathbf{w}$, the transition matrix of the master equation is also irreducible

   $\implies$ there exists a unique globally stable stationary solution.

2. The nonlinear mean-field (rate) equations will generally have multiple attractors – multistability.

3. Convergence of $P(\mathbf{n}, t)$ to a unique steady state implies that fluctuations induce transitions between basins of attraction of fixed points of mean-field equations. For large N the transition rates $\sim \mathrm{e}^{-N\tau}$ for some τ – metastability

4. Buice and Cowan use a different scaling: they interpret u_k in rate equation as the **number** rather than fraction of active neurons in kth population and take transition rates to be

$$T_{k,-1}(\mathbf{n}) = \alpha \mathbf{n}_k, \quad T_{k,+1}(\mathbf{n}) = F\left(\sum_l w_{kl} n_l\right)$$

1. Away from critical points can analyze effects of fluctuations using a Van Kampen system-size expansion in N^{-1}
2. Linear-noise (Gaussian) approximation – Gaussian fluctuations about a deterministic trajectory of mean field equations
3. System–size expansion to higher orders in N^{-1} generates correction to MFT in which the mean field couples to higher–order moments – equivalent to carrying out a loop expansion of the Buice–Cowan path integral (PCB SIAM 2009)
4. The system size expansion breaks down close to critical points eg. where a fixed point of mean-field equation becomes marginally stable – critical slowing down
5. System-size expansion cannot account for exponentially small transition rates between metastable states
6. Alternative approach is to use a WKB approximation and analyze the effects of fluctuations for large N using an effective Hamiltonian dynamical system

Part II. Linear–noise (Gaussian) approximation

Perform the change of variables

$$(n_k, t) \to (Nu_k(t) + \sqrt{N}\xi_k, t)$$

where $\mathbf{u}(t)$ is a solution of the mean–field WC equations

Then $\xi_k(t)$ satisfies the Langevin equation

$$\frac{d\xi_k}{dt} = \sum_l A_{kl}(\mathbf{u}(t))\xi_l + \eta_k(t),$$

where $\eta_k(t)$ represents a Gaussian process with zero mean and correlation function

$$\langle \eta_k(t)\eta_l(t')\rangle = B_k(\mathbf{u}(t))\delta_{k,l}\delta(t-t')$$

and

$$A_{kl}(\mathbf{u}) = \frac{\partial H_k(\mathbf{u})}{\partial u_l}$$

$$B_k(\mathbf{u}) = N^{-1}[T_{k,+}(N\mathbf{u}) + T_{k,-}(N\mathbf{u})] = \alpha u_k + F\left(\sum_l w_{kl}u_l\right)$$

Probability density $P(\xi, t)$ satisfies the FP equation

$$\frac{\partial P}{\partial t} = -\sum_{k,l} A_{kl}(\mathbf{u}(t)) \frac{\partial}{\partial \xi_k} [\xi_l P(\boldsymbol{\xi}, t)] + \frac{1}{2} \sum_{k=E,I} B_k(\mathbf{u}(t)) \frac{\partial^2}{\partial \xi_k^2} P(\boldsymbol{\xi}, t)$$

Solution is given given by the multidimensional Gaussian

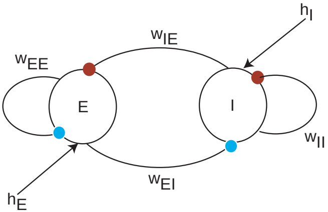
$$P(\boldsymbol{\xi}, t) = \frac{1}{\sqrt{(2\pi)^M \det \mathbf{C}(t)}} \exp\left(-\sum_{k,l} \xi_k C_{kl}^{-1}(t) \xi_l \right)$$

with the covariance matrix satisfying the equation

$$\frac{\partial \mathbf{C}}{\partial t} = \mathbf{A}(\mathbf{u})\mathbf{C} + \mathbf{C}\mathbf{A}(\mathbf{u})^T + \mathbf{B}(\mathbf{u}).$$

Consider an E-I network given by the pair of Wilson-Cowan equations

$$\frac{du_E}{dt} = -u_E + F\left(w_{EE}u_E - w_{EI}u_I + h_E\right)$$
$$\frac{du_I}{dt} = -u_I + F\left(w_{IE}u_E - w_{II}u_I + h_I\right),$$



Let (ν_E^*, ν_I^*) denote a fixed point with associated Jacobian

$$\mathbf{J} = \alpha \begin{pmatrix} -1 + w_{EE}\nu_E^*(1-\nu_E^*) & -w_{EI}\nu_E^*(1-\nu_E^*) \\ w_{IE}\nu_I^*(1-\nu_I^*) & -1 - w_{II}\nu_I^*(1-\nu_I^*) \end{pmatrix}$$

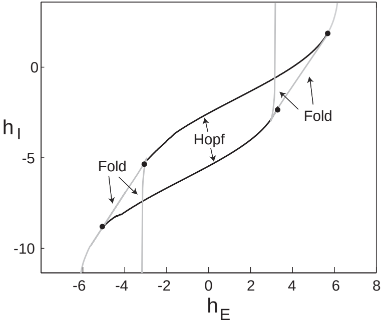
assuming F is a sigmoid with $F' = F(1-F)$

Phase diagram in the (h_E, h_I)–plane for a fixed weight matrix w

Fixed point will be stable provided that the eigenvalues $\lambda_\pm$ of $\mathbf{J}$ have negative real parts

$$\lambda_\pm = \frac{1}{2}\left(\mathrm{Tr}\,\mathbf{J} \pm \sqrt{[\mathrm{Tr}\,\mathbf{J}]^2 - 4\mathrm{Det}\,\mathbf{J}}\right).$$

This leads to the stability conditions $\mathbf{Tr}\,\mathbf{J} < 0$ and $\mathrm{Det}\,\mathbf{J} > 0$.



Hopf bifurcation curves satisfy $\mathrm{Tr} = 0$ with $\mathrm{Det}\,\mathbf{J} > 0$.

Saddle–node bifurcation curves given by the condition $\mathrm{Det}\,\mathbf{J} = 0$ with $\mathrm{Tr}\,\mathbf{J} < 0$.

Power spectrum for stochastic E-I network

Taking Fourier transforms of Langevin equation in linear noise approximation

$$-i\omega\widetilde{\xi}_k(\omega) = \sum_{l=E,I} A_{kl}\widetilde{\xi}_l(\omega) + \widetilde{\eta}_k(\omega).$$

This can be rearranged to give

$$\widetilde{\xi}_k(\omega) = \sum_{l=E,I} \Phi^{-1}_{kl}(\omega)\widetilde{\eta}_l(\omega), \quad \Phi_{kl}(\omega) = -i\omega\delta_{k,l} - A_{kl}.$$

The Fourier transform of the Gaussian process $\eta_k(t)$ has the correlation function

$$\langle\widetilde{\eta}_k(\omega)\widetilde{\eta}_l(\omega)\rangle = 2\pi B_k(\mathbf{u}^*)\delta_{k,l}\delta(\omega+\omega').$$

The power spectrum is defined according to

$$2\pi\delta(0)P_k(\omega) = \langle|\widetilde{\xi}_k(\omega)|^2\rangle,$$

so that

$$P_k(\omega) = \sum_{l=E.I} |\Phi^{-1}_{kl}(\omega)|^2 B_l(\mathbf{u}^*).$$

Noise-amplification of oscillations in an E-I network

Power spectrum can be evaluated explicitly to yield

$$P_k(\omega) = \frac{\beta_k + \gamma_k \omega^2}{|D(\omega)|^2}$$

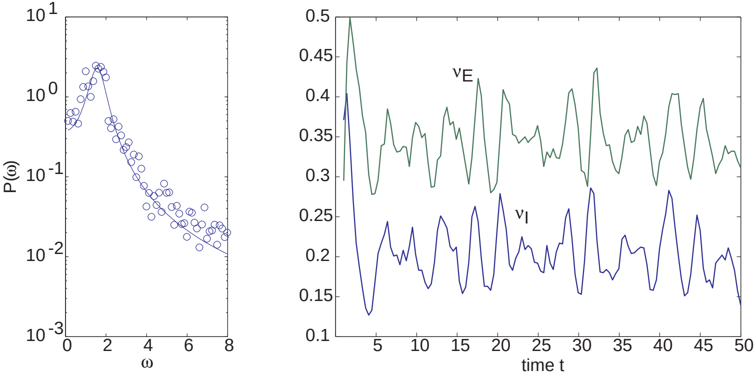
with $D(\omega) = \mathrm{Det}\, \Phi(\omega) = -\omega^2 + i\omega \mathrm{Tr}\, \mathbf{J} + \mathrm{Det}\, \mathbf{J}$ and

$$\beta_E = J_{22}^2 B_E(\mathbf{u}^*) + J_{12}^2 B_I(\mathbf{u}^*), \quad \gamma_E = B_E(\mathbf{u}^*)$$
$$\beta_I = J_{21}^2 B_E(\mathbf{u}^*) + J_{11}^2 B_I(\mathbf{u}^*), \quad \gamma_I = B_I(\mathbf{u}^*).$$

Evaluating the denominator and using the stability conditions $\mathrm{Tr}\, \mathbf{J} < 0$, $\mathrm{Det}\, \mathbf{J} > 0$,

$$P_k(\omega) = \frac{\beta_k + \gamma_k \omega^2}{(\omega^2 - \Omega_0^2)^2 + \Gamma^2 \omega^2}$$

where $\Gamma = \mathrm{Tr}\, \mathbf{J}$ and $\Omega_0^2 = \mathrm{Det}\, \mathbf{J}$.



Suppose that the fixed point of mean-field equation is a focus (damped oscillations)

Find that there is a resonance in the power spectrum around the subthreshold frequency

Analogous to previous studies of noise-amplification of biochemical oscillations in cells (McKane et al 2007).

Part III. WKB approximation and rare event statistics

Let Ω denote the basin of attraction of a stable fixed point S of the mean–field equations with boundary $\partial\Omega$ (separatrix between basins of attraction)

Let $P_0(\mathbf{x})$ be the slowest decaying eigensolution of the rescaled master equation

$$\sum_{k=1}^{M}\sum_{r=\pm 1}\left[T_{k,r}(\mathbf{x}-r\mathbf{e}_k/N)P_0(\mathbf{x}-r\mathbf{e}_k/N,t)-T_{k,r}(\mathbf{x})P_0(\mathbf{x},t)\right]=\lambda_0 P_0(\mathbf{x},t).$$

with appropriate BCs on $\partial\Omega$, where $\mathbf{x}=\mathbf{n}/N$ such that

$$T_{k,-1}(\mathbf{x})=\alpha x_k,\;\; T_{k,+1}(\mathbf{n})=F\left(\sum_l w_{kl}x_l+h_k\right).$$

Lifetime of metastable state is given by $\tau=\lambda_0^{-1}$ with

$$\lambda_0=\frac{\int_{\partial\Omega}\mathbf{n}(\mathbf{x})\cdot\mathbf{J}(\mathbf{x})d\mathbf{x}}{\int_\Omega P_0(\mathbf{x})d\mathbf{x}}$$

Here $\mathbf{n}(\mathbf{x})$ is the unit normal to the boundary $\partial\Omega$ at $\mathbf{x}$ and $J(\mathbf{x})$ is the probability flux on boundary

WKB approximation (Freidlin and Wentzell, Ludwig, Matkowsky and Schuss, Maier and Stein, Talkner ...)

For large N, $\lambda_0 \sim \mathrm{e}^{-NE_0}$ with $E_0 = \mathcal{O}(1)$.

Can treat $P_0(\mathbf{n})$ as a solution to the stationary master equation – quasistationary solution

Take $P_0(\mathbf{x})$ within Ω to have the WKB form

$$P_0(\mathbf{x}) \sim K(\mathbf{x})\mathrm{e}^{-NW(\mathbf{x})}, \quad K(S) = 1, W(S) = 0,$$

In order to satisfy boundary conditions on $\partial\Omega$, use asymptotic expansions to match with an inner solution in a boundary layer near the separatrix $\partial\Omega$.

This will determine the probability flux vector $\mathbf{J}(\mathbf{x})$ and hence λ_0.

Substituting the WKB approximation into the stationary master equation and balancing coefficients of powers of N^{-1} yields equations for W, K

Hamilton–Jacobi equation for W

$$H(\mathbf{x},\mathbf{p}) \equiv \sum_{r=\pm 1}\sum_{k=1}^{M} T_{k,r}(\mathbf{x})\left[\mathrm{e}^{rp_k}-1\right]=0, \qquad p_k=\frac{\partial W}{\partial x_k}$$

Classical mechanics interpretation: $(\mathbf{x},\mathbf{p})$ are position and momentum vectors of a particle $\mathbf{x}\in\Omega$ with trajectories given by solution of Hamilton's equations

$$\dot{x}_k=\frac{\partial H}{\partial p_k}=\sum_{r=\pm 1} rT_{k,r}(\mathbf{x})\mathrm{e}^{rp_k}$$

$$\dot{p}_k=-\frac{\partial H}{\partial x_k}=\sum_{r=\pm 1}\sum_{l=1}^{M}\frac{\partial T_{l,r}}{\partial x_k}(\mathbf{x})\left[\mathrm{e}^{rp_l}-1\right]$$

W is a solution to a Hamilton-Jacobi equation so that

$$W(\mathbf{x})=\int_S^{\mathbf{x}} p(\mathbf{x}')\cdot d\mathbf{x}',$$

where the line integral is taken along a zero–energy trajectory of Hamilton's equations

Can also solve for K by integrating along zero energy trajectories:

$$\dot{K} \equiv \sum_i \frac{\partial H}{\partial p_i}\frac{\partial K}{\partial x_i} = -\left[\sum_i \frac{\partial^2 H}{\partial p_i \partial x_i} + \frac{1}{2}\sum_{i,j} Z_{ij}\frac{\partial^2 H}{\partial p_i \partial p_j}\right] K,$$

where $Z_{ij} = \partial_i \partial_j W(\mathbf{x})$ is the Hessian matrix of $W(\mathbf{x})$

It can be shown by successive differentiation of the HJ equations that

$$\dot{Z}_{ij} = -\left[\sum_{k,l} \frac{\partial^2 H}{\partial p_k \partial p_l} Z_{ik} Z_{jl} + \sum_l \frac{\partial^2 H}{\partial x_i \partial p_l} Z_{jl} + \sum_l \frac{\partial^2 H}{\partial x_j \partial p_l} Z_{il} + \frac{\partial^2 H}{\partial x_i \partial x_j}\right].$$

Suppose that the deterministic network has two stable fixed points separated by a saddle point Q on $\partial\Omega$

In this case the most probable path from S to $\partial\Omega$ is through Q and the behavior around Q dominates the matched asymptotics.

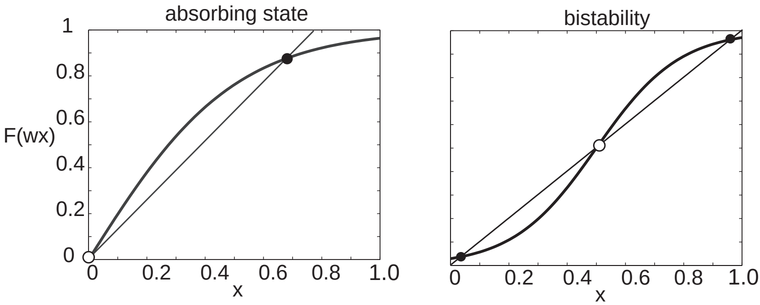
It can then be shown that the transition rate takes the form

$$\lambda_0 = \frac{\lambda_+(Q)}{2\pi}\left[\frac{\det \mathbf{Z}(S)}{\det \mathbf{Z}(Q)}\right]^{1/2} K(Q)\mathrm{e}^{-W(Q)/N},$$

where $\lambda_+(Q)$ is the positive eigenvalue of the Jacobian obtained by the linearizing the mean–field equation about Q.

Mean–field equation

$$\frac{dx}{dt} = -x + F(wx).$$



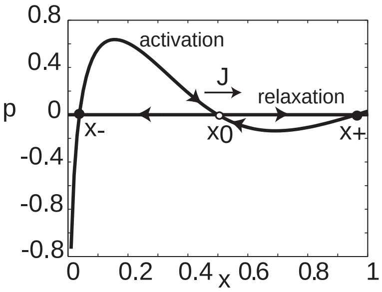
Hamilton–Jacobi equation

$$H(x,p) = \sum_{r=\pm 1} T_r(x)\,[\mathrm{e}^{rp} - 1] = 0, \quad p = \frac{\partial W}{\partial x}$$

with $T_+(x) = F(wx)$, $T_-(x) = \alpha x$

Since HJ equation is a quadratic in e^p, there are two classes of zero–energy solution

$$p = 0, \quad p = p_*(x) \equiv \ln \frac{T_-(x)}{T_+(x)}.$$



Solution of transport equation shows that for zero energy solutions, the quasistationary solution along an activation trajectory takes the form

$$P(x) = \frac{A}{\sqrt{\alpha x F(wx)}} \mathrm{e}^{-NW(x)}, \qquad W(x) = \int^x \ln\left[\frac{\alpha y}{F(wy)}\right] dy$$

Along a relaxation trajectory

$$P(x) = \frac{B}{F(wx) - \alpha x}$$

Undetermined constants and flux J obtained by matching solutions with Gaussian approximation around saddle point x_0.

Find that exit time from metastable state around x_- is

$$\tau = \frac{2\pi}{\sqrt{-\alpha + wF'(wx_0)}} \frac{1}{\sqrt{|-\alpha + wF'(wx_-)|}} \sqrt{\frac{x_0}{x_-}} \mathrm{e}^{N[W(x_0) - W(x_-)]}$$

Part IV. Path-integral formulation of stochastic neurodynamics

Consider the representation of the joint probability density for the fields $\mathbf{\Phi}_i = \{\Phi_i(s), 0 \leq s \leq t\}$, with $\Phi_i = N u_i$ and u_i satisfying the deterministic rate equation.

Can be written formally as an infinite product of Dirac delta functions that enforce the solution of the rate equation at each point in time:

$$P[\mathbf{\Phi}] = \mathcal{N} \prod_{s \leq t} \prod_i \delta \left(\partial_t \Phi_i + \alpha \Phi_i - NF\left(\sum_j w_{ij} \Phi_j / N \right) - \delta(t) \Phi_i^{(0)} \right),$$

where $\mathcal{N}$ is a normalization factor and have the initial condition $\Phi_i(0) = \Phi_i^{(0)}$.

Introduce the Fourier representation of the Dirac delta function:

$$P[\mathbf{\Phi}] = \int \prod_i D\widetilde{\mathbf{\Phi}}_i \mathrm{e}^{-S[\mathbf{\Phi}, \widetilde{\mathbf{\Phi}}]}, \qquad D\widetilde{\mathbf{\Phi}}_i \sim \mathcal{N} \prod_{s \leq t} d\widetilde{\Phi}_i(s)$$

where each $\tilde{\Phi}_i(s)$ is integrated along the imaginary axis, and S is the so–called action

$$S[\mathbf{\Phi}, \widetilde{\mathbf{\Phi}}] = \int dt \sum_i \widetilde{\Phi}_i(t) \left[\partial_t \Phi_i + \alpha \Phi_i - NF\left(\sum_j w_{ij} \Phi_j / N \right) \right] - \sum_i \widetilde{\Phi}_i(0) \Phi_i^{(0)}.$$

Path integral representation persists when fluctuations are taken into account, with modified action

$$S[\Phi,\widetilde{\Phi}] \quad = \quad \int dt \sum_i \widetilde{\Phi}_i \left[\partial_t \Phi_i + \alpha\Phi_i - N\widehat{F}\left(\sum_j w_{ij}\Psi_j/N\right)\right] - \sum_i \widetilde{\Phi}_i(0)\Phi_i^{(0)},$$

where $\Psi_j = \widetilde{\Phi}_j\Phi_j + \Phi_j$ and, for simplicity, the initial distribution is given by a product of independent Poisson processes with means $\overline{n}_i = \Phi_i^{(0)}$,

$$P(\mathbf{n},0) = \frac{[\overline{n}_i]^{n_i}\mathrm{e}^{-\overline{n}_i}}{n_i!}.$$

$\widehat{F}$ is obtained from the gain function F after "normal–ordering" the action: move all fields $\widetilde{\Phi}$ to the right of all fields Φ using repeated application of the commutation rule

$$\Phi_i\widetilde{\Phi}_j = \widetilde{\Phi}_j\Phi_i + \delta_{i,j}.$$

Thus, if $g(\Psi) = (\widetilde{\Phi}_i + 1)\Phi_i(\widetilde{\Phi}_j + 1)\Phi_j$ then

$$\widehat{g}(\Psi) = (\widetilde{\Phi}_i + 1)(\widetilde{\Phi}_j + 1)\Phi_i\Phi_j + (\widetilde{\Phi}_i + 1)\Phi_i\delta_{i,j}.$$

Given the probability distribution $P[\Phi]$, we can calculate mean–fields according to

$$\begin{aligned}\langle\langle \Phi_k(t_1)\rangle\rangle &= \int \prod_i D\Phi_i \Phi_k(t_1) P[\Phi] \\ &= \int \prod_i D\Phi_i \int \prod_i D\widetilde{\Phi}_i \; \Phi_k(t_1) \mathrm{e}^{-S[\Phi,\widetilde{\Phi}]}.\end{aligned}$$

Similarly two–point correlations are given by

$$\langle\langle \Phi_k(t_1)\Phi_l(t_2)\rangle\rangle = \int \prod_i D\Phi_i \int \prod_i D\widetilde{\Phi}_i \; \Phi_k(t_1)\Phi_l(t_2) \mathrm{e}^{-S[\Phi,\widetilde{\Phi}]}.$$

In terms of the statistics of the physical activity variables $m_i(t)$ one finds that

$$\langle m_k(t)\rangle \equiv \sum_{\mathbf{n}} n_k P(\mathbf{n},t) = \langle\langle \Phi_k(t)\rangle\rangle,$$

whereas the covariance is given by

$$\langle m_k(t) m_l(t)\rangle - \langle m_k(t)\rangle\langle m_l(t)\rangle = \langle\langle \Phi_k(t)\Phi_l(t)\rangle\rangle - \langle\langle \Phi_k(t)\rangle\rangle\langle\langle \Phi_l(t)\rangle\rangle + \langle\langle \Phi_k(t)\rangle\rangle\delta_{k,l}.$$

Hamiltonian dynamical system obtained by carrying out steepest descents on associated generating functional (PCB09)

$$Z[\mathbf{J}] = \int \prod_i D\phi_i \int \prod_i D\widetilde{\phi}_i \mathrm{e}^{-NS[\phi,\widetilde{\phi}]} e^{N\int dt \sum_j J_j(t)\phi_j(t)}$$

after performing the rescalings $\Phi_i \to \phi_i = \Phi_i/N$ so that

$$S[\phi,\widetilde{\phi}] = \int dt \left[\sum_i \widetilde{\phi}_i \partial_t \phi_i - \mathcal{H}(\phi,\widetilde{\phi})\right] - \sum_i \widetilde{\phi}_i(0)\phi_i^{(0)},$$

with

$$\mathcal{H}(\phi,\widetilde{\phi}) = \sum_i \widetilde{\phi}_i \left[-\alpha\phi_i + \widehat{F}\left(\sum_j w_{ij}\phi_j[\widetilde{\phi}_j + 1]\right)\right]$$

In the limit $N \rightarrow \infty$, the path integral is dominated by the "classical" solutions $\mathbf{u}(t), \widetilde{\mathbf{u}}(t)$, which extremize the exponent of the generating functional:

$$\left.\frac{\delta S[\phi,\widetilde{\phi}]}{\delta \phi_i(t)}\right|_{\widetilde{\phi}=\widetilde{\mathbf{u}},\phi=\mathbf{u}} = 0, \quad \left.\frac{\delta S[\phi,\widetilde{\phi}]}{\delta \widetilde{\phi}_i(t)}\right|_{\widetilde{\phi}=\widetilde{\mathbf{u}},\phi=\mathbf{u}} = 0.$$

These equations reduce to

$$\frac{\partial u_i}{\partial t} = \frac{\partial \mathcal{H}(\mathbf{u},\widetilde{\mathbf{u}})}{\partial \widetilde{u}_i}, \quad \frac{\partial \widetilde{u}_i}{\partial t} = -\frac{\partial \mathcal{H}(\mathbf{u},\widetilde{\mathbf{u}})}{\partial u_i}.$$

Recover previous Hamiltonian equations under canonical transformation

$$\widetilde{u}_i = \mathrm{e}^{p_i} - 1, \quad u_i = x_i \mathrm{e}^{-p_i}$$

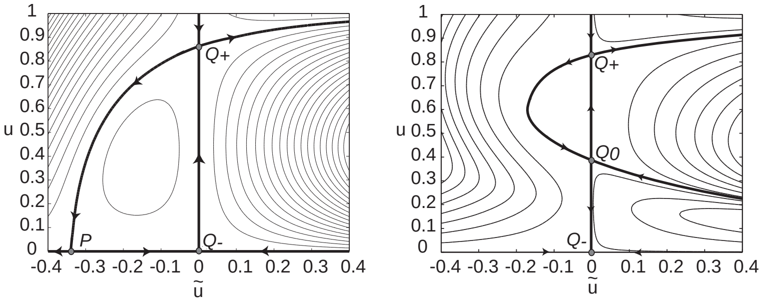
$$\mathcal{H}(\phi, \widetilde{\phi}) = \alpha\widetilde{\phi}\phi - \alpha\widetilde{\phi}F(w[\phi\widetilde{\phi} + \phi]).$$

This leads to the Hamiltonian dynamical system

$$\frac{du}{dt} = \frac{\partial \mathcal{H}}{\partial \widetilde{u}} = -u + F(wu(\widetilde{u}+1)) + \widetilde{u}uwF'(wu(\widetilde{u}+1))$$

and

$$\frac{d\widetilde{u}}{dt} = -\frac{\partial \mathcal{H}}{\partial u} = \widetilde{u}\left(1 - (\widetilde{u}+1)wF'(wu(\widetilde{u}+1))\right).$$



1. P. C. Bressloff. *Statistical neural field theory and the system size expansion.* SIAM J. Appl. Math (2009).
2. P. C. Bressloff. *On the master equation approach to stochastic neurodynamics.* (2010)

OCCAM

OXFORD CENTRE FOR COLLABORATIVE APPLIED MATHEMATICS

THE ROYAL SOCIETY

NSF