

Nonlocal coupling among oscillators mediated by a diffusing substance

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Introduction

- there are many problems in physical chemistry and biology involving the interaction among individuals mediated by the diffusion of some chemical in the medium
- this chemical is both released and absorbed by the individuals, often depending on dynamical processes occurring within them
- the release, diffusion and absorption processes create a long-range coupling among individuals that affects their dynamics
- in this work we explore the consequences of this basic idea into models of non-locally coupled nonlinear oscillators
- coupling problems typically involve more than one timescale

Ovarian cycles

- surge of luteinizing hormone from the anterior pituitary
- LH luteinizes several follicles in the ovary causing each to rupture and release its effective
- at the site of rupture a *corpus luteum* forms and secretes progesterone
- just after ovulation a new set of follicles begins to mature and releases estrogen (ovarian steroid)
- estrogen primes the system for another surge of LH
- cycle period = 28 days for humans

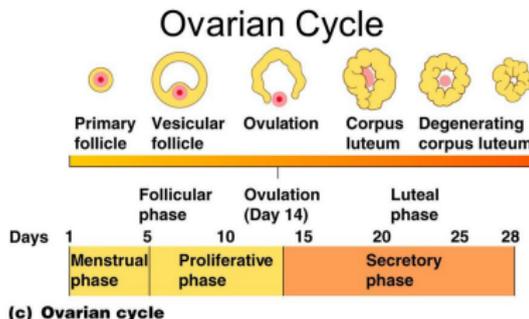
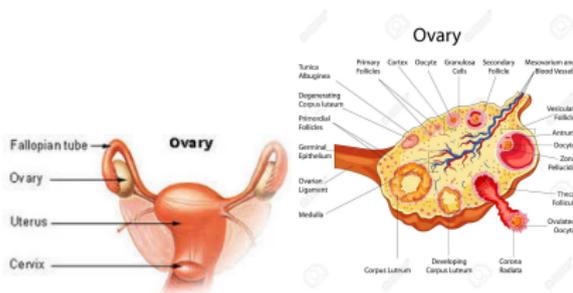


Figure 16.12c

Synchronization of ovarian cycles

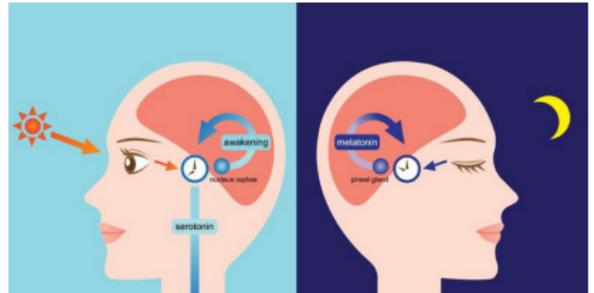
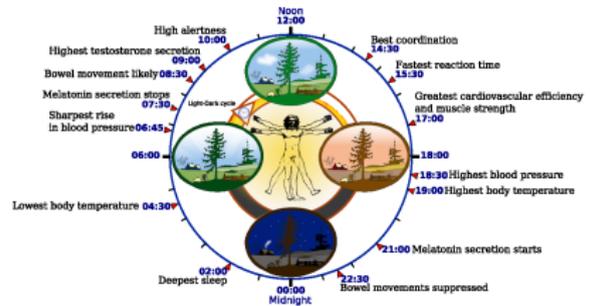
J. Schank and M. McClintock, *J. Theor. Biol.* **157**, 317 (1992)

- McClintock effect: women that live together synchronize their ovarian cycles
- the synchronization of ovarian cycles is mediated by airborne chemosignals called pheromones
- two distinct chemicals: one advances and another delays the phase of the ovarian cycle
- pheromones diffuse in the atmosphere: there must be a common air supply

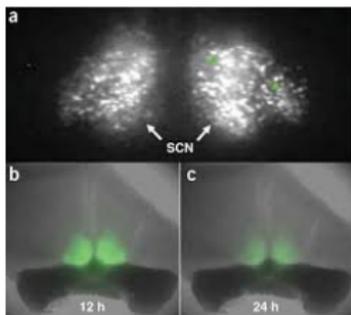
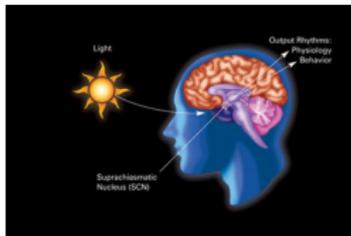


Circadian rhythms

- biological processes displaying an endogenous oscillation of about 24 hours (“circa diem”)
- present in animals, plants, fungi, and cyanobacteriae
- these 24-hour rhythms are driven by circadian clock cells
- circadian rhythms can be adjusted (entrained) to the local environment by external cues (zeitgebers)



Suprachiasmatic nucleus



- region of the brain (hypothalamus) responsible for controlling circadian rhythms
- receives input from specialized photosensitive ganglion cells in the retina
- maintains control by synchronizing their own near-24-hour rhythms and control circadian phenomena in local tissues
- it contains around 20,000 neurons (clock cells)
- collective rhythm possible because of frequency synchronization induced by coupling among clock cells
- coupling is mediated by a neurotransmitter (GABA) diffusing through intercell medium

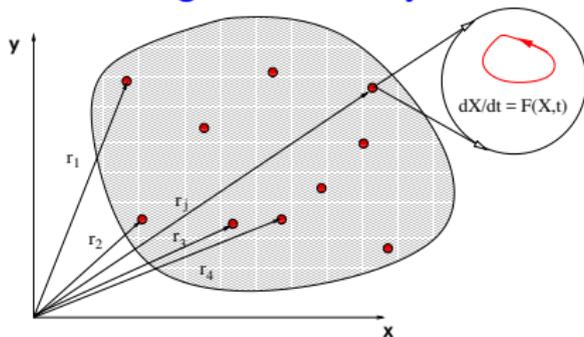
Chemotaxis of *Dictyostelium*

- chemotaxis: motion of an organism in response to a chemical stimulus
- *Dictyostelium*: amoebae (“slime mold”)
- in absence of food about 10^5 cells release signal molecules of chemoattractant cyclic adenosine monophosphate (cAMP) in the environment
- they can find other cells and move to create clusters (releasing every 6 min during periods reaching 5 to 6 hours after starvation)



Coupling model

Y. Kuramoto, Prog. Theor. Phys. **94**, 321 (1995)



- N pointlike oscillator cells located at \vec{r}_j , ($j = 1, 2, \dots, N$) in a d -dimensional Euclidean space
- each oscillator has an internal dynamics governed by the flux $\mathbf{F}(\mathbf{X}, t)$, where $\mathbf{X} = (x_1, x_2, \dots, x_M)^T$ in a M -dim. phase space
- the time evolution of each oscillator is affected by the local concentration of a chemical $A(\mathbf{r}, t)$

$$\dot{\mathbf{X}}_j = \mathbf{F}(\mathbf{X}_j, t) + \mathbf{g}(A(\vec{r}_j, t))$$

Coupling model in the adiabatic limit

- the concentration satisfies a inhomogeneous diffusion equation

$$\varepsilon \dot{A} = -\eta A + D \nabla^2 A + \sum_k h(\mathbf{X}_k) \delta(\vec{r} - \vec{r}_k)$$

- η : coefficient of chemical degradation, D : diffusion coefficient
- $\varepsilon \approx 0$: diffusion timescale much faster than oscillator period
- concentration fast-relaxes to a stationary value

$$A(\vec{r}_j) = \sum_k \sigma(\vec{r}_j - \vec{r}_k) h(\mathbf{X}_k)$$

- $\sigma(\mathbf{r})$ is the Green function of the diffusion equation

$$(\eta - D \nabla^2) \sigma(\vec{r}_j - \vec{r}) = \delta(\vec{r}_j)$$

- chemical coupling in the adiabatic limit

$$\dot{\mathbf{X}}_j = \mathbf{F}(\mathbf{X}_j, t) + \sum_k \sigma(\vec{r}_j - \vec{r}_k) \mathbf{g}(h(\mathbf{X}_k)).$$

Types of chemical coupling

- linear coupling: $\mathbf{g}(h(\mathbf{X}_k)) = \mathbf{A}\mathbf{X}_k$
- future coupling: $\mathbf{g}(h(\mathbf{X}_k)) = \mathbf{A}\mathbf{F}(\mathbf{X}_k)$
- nonlinear coupling: $\mathbf{g}(h(\mathbf{X}_k)) = \mathbf{A}\mathbf{H}(\mathbf{X}_k)$
- Green function for isotropic systems ($r \equiv |\vec{r}_j - \vec{r}|$)

$$\sigma(r) = C \begin{cases} \exp(-\gamma r), & \text{if } d = 1, \\ K_0(\gamma r), & \text{if } d = 2, \\ \frac{\exp(-\gamma r)}{\gamma r}, & \text{if } d = 3 \end{cases}$$

- inverse coupling length: $\gamma = \sqrt{\eta/D}$,
- C is determined from the normalization condition $\int d^d r \sigma(\vec{r}) = 1$

Limiting cases

- $\gamma \rightarrow 0$: global type of coupling (all-to-all)

$$\dot{\mathbf{X}}_j = \mathbf{F}(\mathbf{X}_j, t) + \mathbf{A}\bar{\mathbf{X}}$$

- mean field of all oscillators (except itself)

$$\bar{\mathbf{X}} = \frac{1}{N-1} \sum_{k=1, k \neq j}^N \mathbf{X}_k$$

- large γ : local (diffusive) type of coupling (nearest neighbors)

$$\dot{\mathbf{X}}_j = \mathbf{F}(\mathbf{X}_j, t) + \mathbf{A}(\mathbf{X}_{j-1} + \mathbf{X}_{j+1})$$

- varying γ we can pass continuously from global to local coupling (in numerical studies of long-range coupling)

Phase oscillators with chemical coupling

- for phase oscillators $\mathbf{X} \rightarrow \theta$ and $\mathbf{F} \rightarrow \omega$
- nonlinear coupling (extended Kuramoto model)

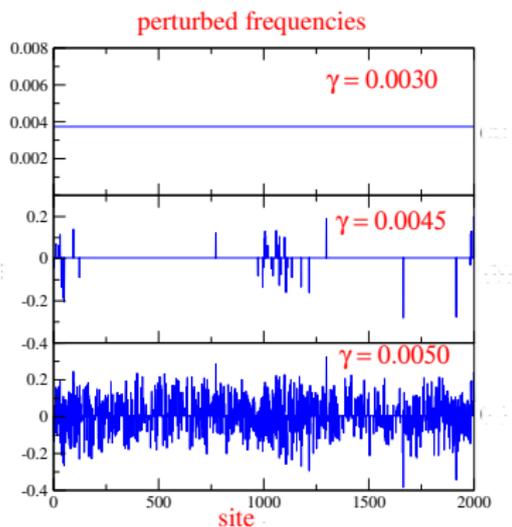
$$\dot{\theta}_j = \omega_j + K \sum_k \sigma(\vec{r}_j - \vec{r}_k) \sin(\theta_k - \theta_j)$$

- for $d = 1$ the Green function is $\sigma(x_i - x_j) = e^{-\gamma|x_i - x_j|}$ with $\gamma = \sqrt{\eta/D}$ (inverse coupling length), and normalization constant determined by $\int dx \sigma(x) = 1$
- one-dimensional lattice with periodic boundary conditions
- normalization factor $\kappa(\gamma) = 2 \sum_{\ell=1}^{N'} e^{-\gamma\ell}$

$$\dot{\theta}_j = \omega_j + \frac{K}{\kappa(\gamma)} \sum_{\ell=1}^{N'} e^{-\gamma\ell} [\sin(\theta_{j-\ell} - \theta_j) + \sin(\theta_{j+\ell} - \theta_j)].$$

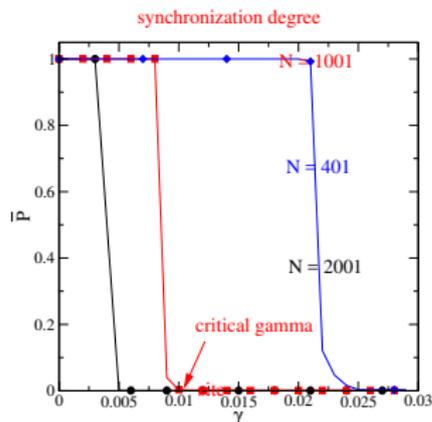
Frequency synchronization

C. Batista *et al.*, Physica A **470**, 236 (2017)



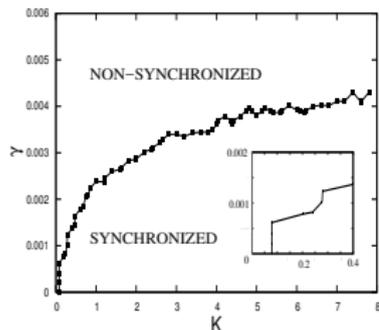
- frequency without coupling: ω_j , randomly chosen according to a zero-mean gaussian PDF $g(\omega)$
- frequency after coupling: $\Omega_j = \dot{\theta}_j$
- small γ : nearly global coupling = complete synchronization
- intermediate γ : partial synchronization
- large γ : nearly local coupling = no synchronization
- competition between disorder and diffusion

Partial frequency synchronization

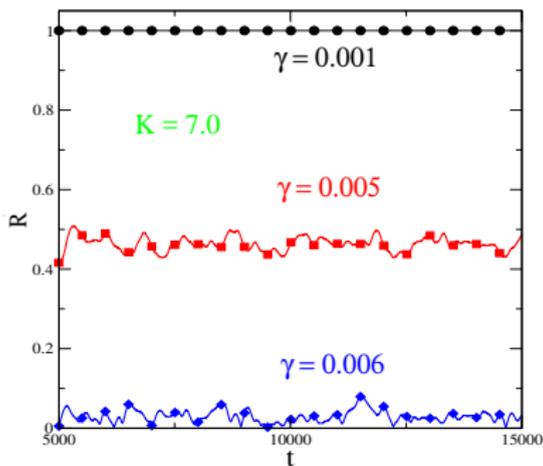


- N_i : length of i th sync plateau
- N_p : number of plateaus
- average plateau size:

$$\langle N \rangle = (1/N_p) \sum_{i=1}^{N_p} N_i$$
- sync degree: $P = \langle N \rangle / N$
- completely sync state: $P = 1$
- completely non-sync state: $P \approx 0$
- critical γ for increasing K
- small K : no sync for any γ
- global coupling ($\gamma = 0$): sync after $K_c = 2/\pi g(0) = 0.08$
- local coupling (large γ): no sync, even with large K



Phase synchronization

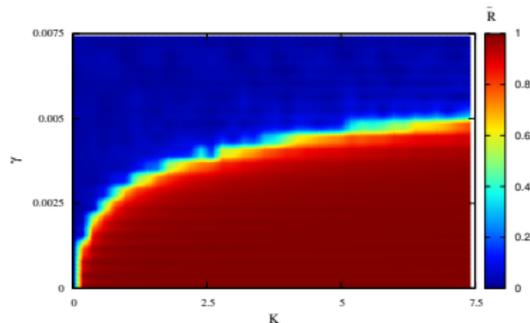
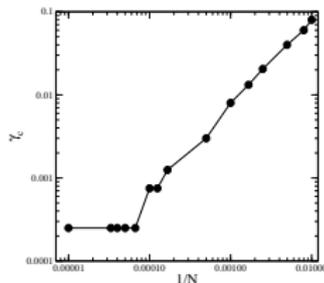
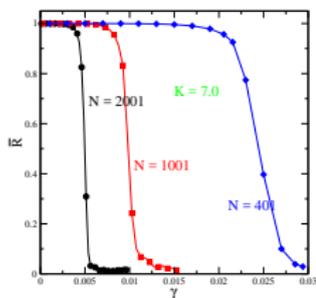


- equality of phases (stronger than frequency sync)
- complex order parameter

$$z(t) = R(t)e^{i\varphi(t)} = \frac{1}{N} \sum_{j=1}^N e^{i\theta_j(t)}$$

- completely synchronized state: $R = 1$, \rightarrow small γ (global)
- non-synchronized state: $R \approx 0$, \rightarrow intermediate γ
- partially synchronized state: $0 < R < 1$, \rightarrow large γ (local)

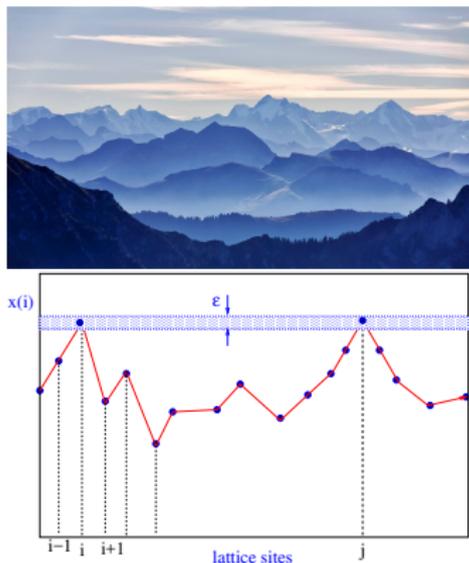
Transition to phase synchronization



- \bar{R} : time-averaged order parameter magnitude
- synchronization transition for a critical γ_c (fixed K)
- γ_c decreases with increasing lattice size N
- thermodynamical limit ($N \rightarrow \infty$): $\gamma_c = 0.00025$
- coupling parameter plane: deep blue: no phase sync, red: complete phase sync

Spatial recurrence matrix

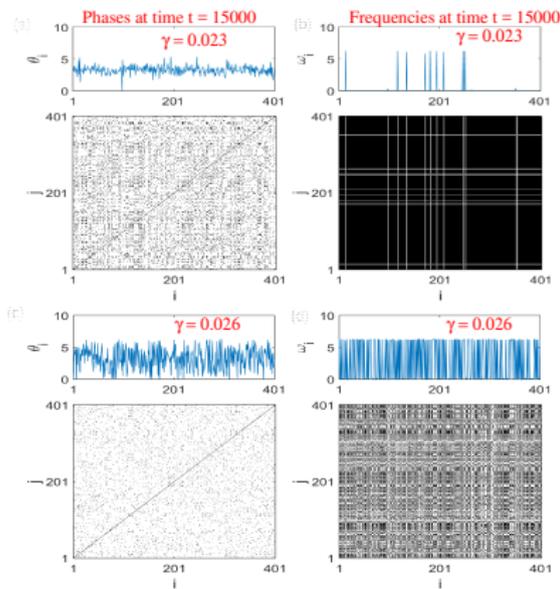
D. Vasconcelos *et al.*, Phys. Rev. E **73**, 56207 (2006)



- a tool for characterization of complex spatial patterns
- one-dimensional spatial pattern with N sites: $\{x_k\}$, $k = 0, \dots, N$
- spatial recurrence: two sites i and j have the same height, up to some precision ε
- spatial recurrence matrix: $R_{ij} = 1$ if $|x_i - x_j| \leq \varepsilon$, and 0 otherwise

$$R_{ij} = \Theta(|x_i - x_j| - \varepsilon)$$

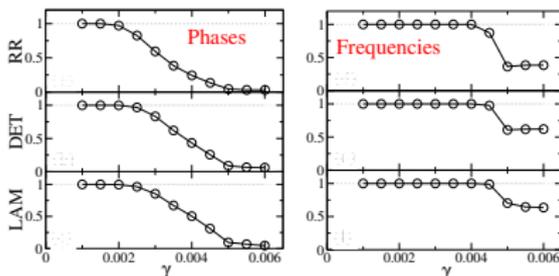
Spatial recurrence plots



- spatial recurrence plot: graphical representations of the spatial recurrence matrix with elements R_{ij}
- characterizes the existence of spatially homogeneous (synchronized) states in phase and frequency
- characterizes the existence of spatially inhomogeneous states (chimeras)

Recurrence quantification analysis

M. Santos *et al.*, Phys. Lett. A **379**, 2128 (2015)



- recurrence rate: fraction of recurrent points: $RR = \frac{1}{N^2} \sum_{i,j} R_{ij}$
- determinism: fraction of points belonging to diagonal structures
- laminarity: fraction of points belonging to horizontal structures
- transitions to phase and frequency synchronization as γ is varied from large (short range) to small (long range)

Model for biological clock cells

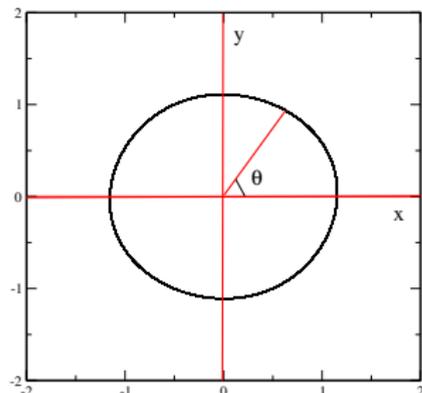
R. Kronauer *et al.*, J. Biol. Rhythms **14**, 501 (1999)

- model for coupled circadian clock cells in the SCN
- each clock cell with its own period $\tau_j \approx 24h$ (Gaussian PDF)
- Van der Pol-type oscillator describing the clock cell dynamics

$$\mathbf{X}_j = \frac{12}{\pi} \begin{pmatrix} x_j \\ y_j \end{pmatrix}, \mathbf{F}(\mathbf{X}_j, t) = \begin{pmatrix} y_j + \epsilon \left(x_j - \frac{4}{3} x_j^3 \right) + B(t) - C_x x_j \\ - \left(\frac{24}{\tau_j} \right)^2 x_j + B(t) y_j - C_y y_j \end{pmatrix}$$

- $C_{x,y}$ are coupling parameters
- photic stimulation (zeitgeber): $B(t) = C (1 - m \langle x \rangle) [I(t)]^{1/3}$
- spatial average: $\langle x \rangle = (1/N) \sum_{i=1}^N x_i$

Phase and frequency of clock cells



- oscillator dynamics displays a limit cycle encircling the origin
($x_{k0} = 0, y_{k0} = 0$)
- geometrical phase

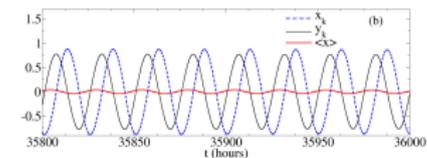
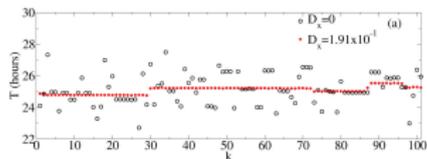
$$\theta_k(t) = \arctan \left(\frac{y_k(t) - y_{k0}}{x_k(t) - x_{k0}} \right)$$

- oscillator frequency and period

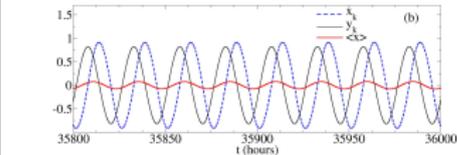
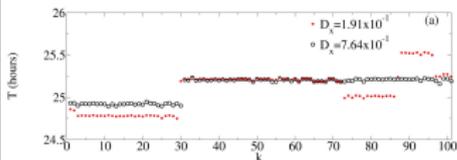
$$\Omega_k = \frac{2\pi}{T_k} = \lim_{T \rightarrow \infty} \frac{\theta_k(T) - \theta_k(0)}{T}$$

Synchronization of clock cells under constant darkness

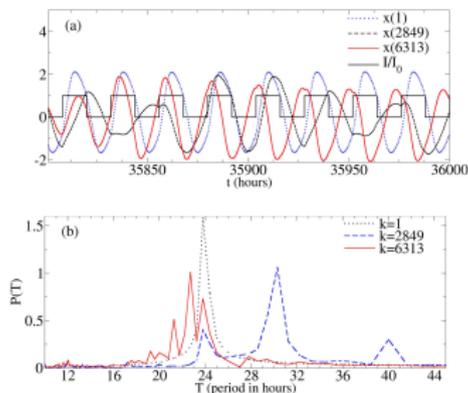
F. Silva *et al.*, CNSNS **35**, 37 (2016)



- system is evolved in constant darkness ($I = 0$)
- top: (a) distribution of periods of SCN cells with $\gamma = 1$ for $D_x = 0$ (open circles) and 0.191 (open circles)
- (b) time series for the x and y variables of one typical SCN cell and mean field $\langle x \rangle$
- bottom: D_x increased to 7.64×10^{-1} (open circles)

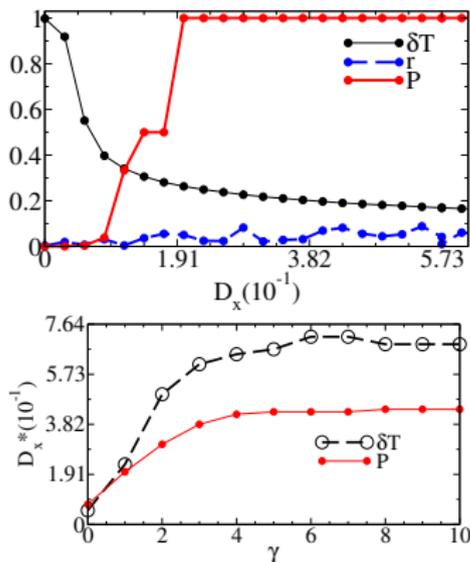


Synchronization of clock cells under dark-bright cycles



- system experiences dark-bright cycles of duration $\Delta t = 12h$ and constant light intensity $I_0 = 1000$
- top: (a) time series for the x variables of three SCN cells selected out of a lattice with 10201 cells with $\gamma = 1$ for $D_x = 7.64 \times 10^{-3}$
- (b) power spectra of the response of the three cells depicted in (a)

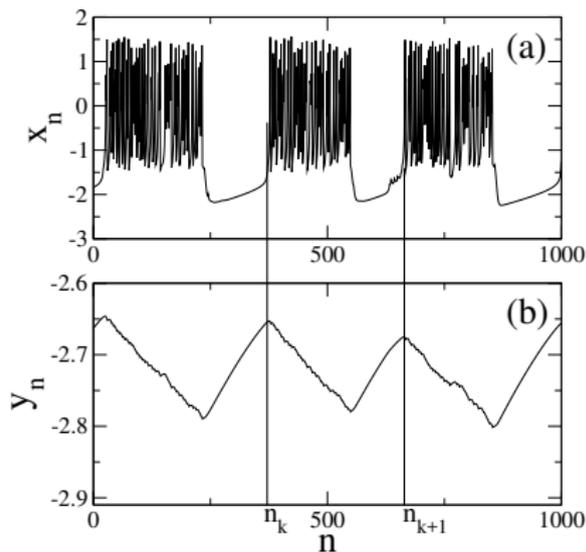
Transition to period synchronization of clock cells



- top: dependence of the period dispersion (black), order parameter magnitude (blue) and synchronization degree (red) with the coupling strength
- D_x^* : critical coupling strength for onset of period synchronization
- bottom: critical coupling strength vs. exponent γ considering the behavior of the period variance (black) and synchronization degree (red).

Autonomous bursting: the Rulkov map

N. Rulkov, Phys. Rev. E **65**, 41922 (2002)



- x_n : “action potential” (fast)
- y_n : “modulating variable” (slow)

$$x_{n+1} = \frac{\alpha}{1 + x_n^2} + y_n$$

$$y_{n+1} = y_n - \sigma x_n - \beta$$

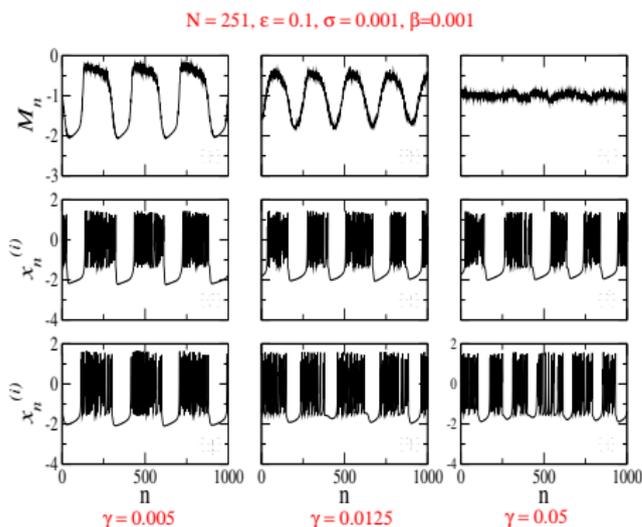
- bursting phase

$$\varphi(n) = 2\pi k + 2\pi \frac{n - n_k}{n_{k+1} - n_k}$$

- bursting frequency $\Omega = \dot{\varphi}$

Bursting synchronization

R. L. Viana *et al.*, CNSNS **17**, 2924 (2012)



- coupled Rulkov maps

$$x_{n+1}^{(j)} = \frac{\alpha^{(j)}}{1 + (x_n^{(j)})^2} + y_n^{(j)} +$$

$$+ \epsilon C \sum_{\ell=1}^{N'} e^{-\gamma \ell} \left[x_n^{(j-\ell)} + x_n^{(j+\ell)} \right]$$

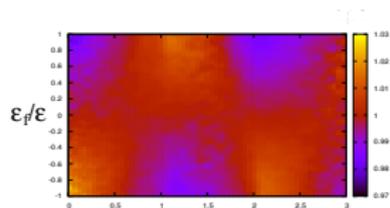
$$y_{n+1}^{(j)} = y_n^{(j)} - \sigma x_n^{(j)} - \beta$$

- parameter α randomly distributed in $[4.1, 4.3]$
- mean field of the lattice

$$M_n = \frac{1}{N} \sum_j x_n^{(j)}$$

Suppression of bursting synchronization

M. Rosenblum and A. Pikowsky, Phys. Rev. E **70**, 41904 (2004)

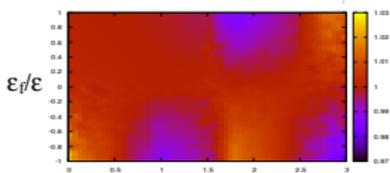


$\gamma = 0.005$

$N = 111$

- delayed feedback control

$$\varepsilon X_n + \varepsilon_f X_{n-\tau}$$

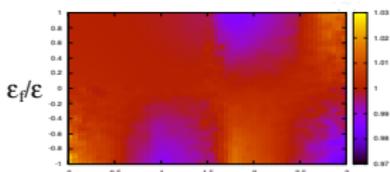


$\gamma = 0.0125$

$\varepsilon = 0.1$

- weighted mean field

$$X_n = C \sum_{\ell=1}^{N'} e^{-\gamma \ell} \left(x_n^{(j-\ell)} + x_n^{(j+\ell)} \right)$$



$\gamma = 0.025$

- suppression coefficient
 $S = \sqrt{\text{var}(X)/\text{var}(X_f)}$

τ/T

Chemical coupling of chaotic maps

- if the local dynamics is governed by a one-dimensional map $x \mapsto f(x)$ we have (future coupling)

$$x_{n+1}^{(i)} = (1 - \varepsilon)f(x_n^{(i)}) + \varepsilon \sum_{j=1}^N \sigma(\vec{r}_i - \vec{r}_j) f(x_n^{(j)}).$$

- non-locally coupled map lattice in one spatial dimension (where $N' = (N - 1)/2$ for N odd)

$$x_{n+1}^{(i)} = (1 - \varepsilon)f(x_n^{(i)}) + \frac{\varepsilon}{\kappa(\gamma)} \sum_{s=1}^{N'} e^{-\gamma s} \left[f(x_n^{(i-s)}) + f(x_n^{(i+s)}) \right],$$

- normalization condition

$$\sum_{k=1}^N \sigma(|\vec{r}_j - \vec{r}_k|) = 1 \Rightarrow \kappa(\gamma) = 2 \sum_{s=1}^{N'} e^{-\gamma s},$$

- periodic boundary conditions: $x_n^{(i \pm N)} = x_n^{(i)}$

Lyapunov spectrum

C. Anteneodo *et al.*, Phys. Lett. A **326**, 277 (2004)

- Lyapunov exponents of a coupled map lattice: $\lambda_k = \ln \Lambda_k$, where $\{\Lambda_k\}_{k=1}^N$ are the eigenvalues of the matrix

$$\hat{\Lambda} = \lim_{n \rightarrow \infty} \left(\tau_n^T \tau_n \right)^{1/2n},$$

- ordered product of the jacobian matrices

$$\tau_n = \mathbf{T}_{n-1} \mathbf{T}_{n-2} \dots \mathbf{T}_1 \mathbf{T}_0, \quad T_n^{(ij)} = \frac{\partial x_{n+1}^{(i)}}{\partial x_n^{(j)}}$$

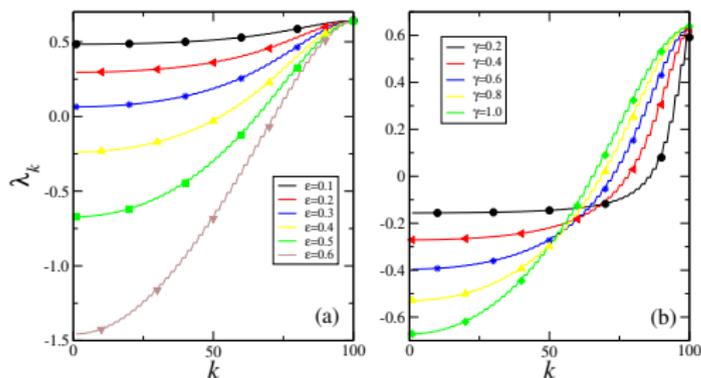
- for the chemical coupling in one spatial dimension

$$T_n^{(ik)} = (1-\varepsilon) f' \left(x_n^{(i)} \right) \delta_{ik} + \frac{\varepsilon}{\kappa(\gamma)} \exp(-\gamma r_{ik}) f' \left(x_n^{(k)} \right) (1-\delta_{ik}),$$

- where $r_{ij} = \min_{\ell} |i - j + \ell N|$

Lyapunov spectrum of coupled Bernoulli maps

R. Viana *et al.*, *Nonlinear Dynamics* **87**, 1589 (2017)



- $f(x) = \beta x, \text{ mod } 1$, strongly chaotic for $\beta > 1$

- Lyapunov spectrum

$$\lambda_k = \ln \beta + \ln \left| \left(1 - \epsilon\right) + \frac{\epsilon}{\kappa(\gamma)} b_k \right|$$

- periodic boundary conditions
→ jacobian matrices are circulant

$$b_k = 2 \sum_{m=1}^{N'} e^{-\gamma m} \cos \left(\frac{2\pi km}{N} \right)$$

Stability of a completely synchronized state

C. Anteneodo *et al.*, Phys. Rev. E **68**, 045202 (2003)

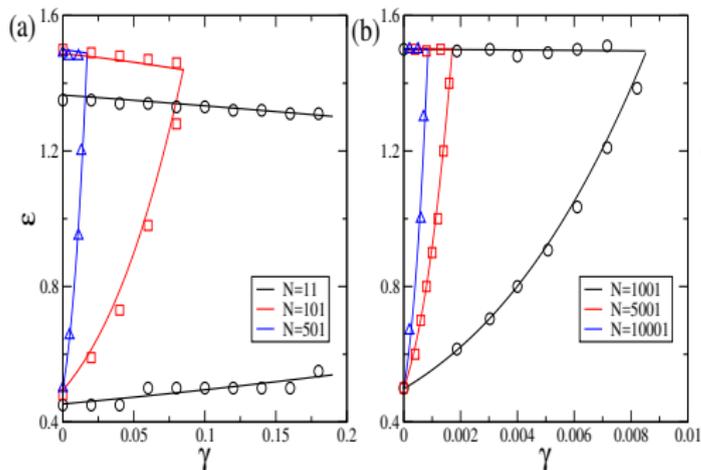
- $x_n^{(1)} = x_n^{(2)} = \dots = x_n^{(N)} = x_n^*$: defines a synchronization manifold \mathcal{S} in the phase space
- Lyapunov spectrum of the completely synchronized state

$$\lambda_k^* = \lambda_U + \ln \left| \left(1 - \varepsilon\right) + \frac{2\varepsilon}{\kappa(\gamma)} \sum_{m=1}^{N'} e^{-\gamma m} \cos\left(\frac{2\pi km}{N}\right) \right|$$

- λ_U : Lyapunov exponent of the uncoupled map
- the completely synchronized state is transversely stable if $\lambda_2^* \leq 0$, such that $\varepsilon_c \leq \varepsilon \leq \varepsilon'_c$, where

$$\varepsilon_c = \left(1 - e^{-\lambda_U}\right) \left(1 - \frac{b_1}{\kappa(\gamma)}\right)^{-1}, \varepsilon'_c = \left(1 + e^{-\lambda_U}\right) \left(1 - \frac{b_{N'}}{\kappa(\gamma)}\right)^{-1}$$

Synchronization of coupled Ulam maps



- Ulam map
 $f(x) = 4x(1 - x)$, $x \in [0, 1)$,
 strongly chaotic ($\lambda_U = \ln 2$)
- completely synchronized state is transversely stable if
 $\epsilon_c \leq \epsilon \leq \epsilon'_c$,

$$\epsilon_c = \frac{1}{2\Delta}, \epsilon'_c = \frac{3}{2\Delta'}$$

$$\Delta = 1 - \frac{b_1}{\kappa(\gamma)}, \Delta' = 1 - \frac{b_{N'}}{\kappa(\gamma)}$$

Conclusions

- oscillator coupling mediated by a diffusing substance reduces, in the one-dimensional case, to an exponentially decaying (non-local) coupling (in the adiabatic limit)
- it allows to pass from a global (all-to-all) to a local (laplacian) coupling by varying a single parameter
- frequency and phase synchronization were analyzed in terms of the coupling parameter plane (strength vs. range)
- transition to frequency and phase synchronization in terms of both K and γ
- recurrence quantification analysis used to characterize phase and frequency spatial patterns
- Lyapunov spectrum can be obtained and it is possible to study the transversal stability of the completely synchronized state

Future work

- in many situations the timescale of diffusion can be compared with the oscillator main period \rightarrow adiabatic approximation no longer holds!
- Kuramoto model for chemical coupling can be generalized for time-dependent interaction kernels
- R. L. Viana and R. P. Aristides: “Nonlocal coupling among oscillators mediated by a slowly diffusing substance”, arXiv:1803.10795 [nlin.AO]
- we can include motion of the oscillators \rightarrow three timescales (oscillator, diffusion and motion): “active molecular dynamics” \rightarrow challenges for computer simulations
- chemotaxis: oscillator motion depends on chemotactic forces, which are proportional to the local gradient of the concentration $\nabla A(\mathbf{r}, t)$

Thank you very much

