Nonlocal coupling among oscillators mediated by a diffusing substance

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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
Synchronization of ovarian cycles


- 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 cyanobacteria
- these 24-hour rhythms are driven by circadian clocks in 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*: amoeabae (“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


- $N$ pointlike oscillator cells located at $\vec{r}_j$, ($j = 1, 2, \cdots N$) in a $d$-dimensional Euclidean space
- each oscillator has an internal dynamics governed by the flux $\mathbf{F}(\mathbf{X}, t)$, where $\mathbf{X} = (x_1, x_2, \ldots x_M)^T$ 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
  \[ \varepsilon \dot{A} = -\eta A + D \nabla^2 A + \sum_k h(X_k) \delta(\vec{r} - \vec{r}_k) \]

- \( \eta \): coefficient of chemical degradation, \( D \): diffusion coefficient
- \( \varepsilon \approx 0 \): diffusion timescale much faster than oscillator period
- concentration fast-relaxes to a stationary value
  \[ A(\vec{r}_j) = \sum_k \sigma(\vec{r}_j - \vec{r}_k) h(X_k) \]

- \( \sigma(\vec{r}) \) 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
  \[ \dot{X}_j = F(X_j, t) + \sum_k \sigma(\vec{r}_j - \vec{r}_k) g(h(X_k)) \]
Types of chemical coupling

- linear coupling: \( g(h(X_k)) = AX_k \)
- future coupling: \( g(h(X_k)) = AF(X_k) \)
- nonlinear coupling: \( g(h(X_k)) = AH(X_k) \)
- 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

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

$$\dot{X}_j = F(X_j, t) + A\overline{X}$$

- mean field of all oscillators (except itself)

$$\overline{X} = \frac{1}{N-1} \sum_{k=1, k \neq j}^{N} X_k$$

- large $\gamma$: local (diffusive) type of coupling (nearest neighbors)

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

- varying $\gamma$ we can pass continuously from global to local coupling (in numerical studies of long-range coupling)
Phase oscillators with chemical coupling

- for phase oscillators $X \rightarrow \theta$ and $F \rightarrow \omega$
- 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


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

perturbed frequencies

$\gamma = 0.0030$

$\gamma = 0.0045$

$\gamma = 0.0050$
Partial frequency synchronization

- $N_i$: length of $i$th sync plateau
- $N_p$: number of plateaus
- average plateau size:
  $$\langle N \rangle = \frac{1}{N_p} \sum_{i=1}^{N_p} N_i$$
- sync degree: $P = \langle N \rangle / N$
- completely sync state: $P = 1$
- completely non-sync state: $P \approx 0$
- critical $\gamma$ for increasing $K$
- small $K$: no sync for any $\gamma$
- global coupling ($\gamma = 0$): sync after $K_c = 2/\pi g(0) = 0.08$
- local coupling (large $\gamma$): 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 \( \gamma \) (global)
- non-synchronized state: \( R \approx 0, \rightarrow \) intermediate \( \gamma \)
- partially synchronized state: \( 0 < R < 1, \rightarrow \) large \( \gamma \) (local)
Transition to phase synchronization

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


- a tool for characterization of complex spatial patterns
- one-dimensional spatial pattern with $N$ sites: $\{x_k\}, k = 0, \ldots, N$
- spatial recurrence: two sites $i$ and $j$ have the same height, up to some precision $\varepsilon$
- 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


- 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 $\gamma$ is varied from large (short range) to small (long range)
Model for biological clock cells


- 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

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

- $C_{x,y}$ 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
  \[\Omega_k = \frac{2\pi}{T_k} = \lim_{T \to \infty} \frac{\theta_k(T) - \theta_k(0)}{T}\]
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 $7.64 \times 10^{-1}$ (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 $\gamma$ considering the behavior of the period variance (black) and synchronization degree (red).
Autonomous bursting: the Rulkov map


- $x_n$: “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

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

\[
x_{n+1}^{(j)} = \frac{\alpha^{(j)}}{1 + (x_n^{(j)})^2} + y_n^{(j)} + \varepsilon C \sum_{\ell=1}^{N'} e^{-\gamma \ell} \left[ x_n^{(j-\ell)} + x_n^{(j+\ell)} \right]
\]

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

- parameter \(\alpha\) 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


- delayed feedback control
  \[ \varepsilon X_n + \varepsilon_f X_{n-\tau} \]

- weighted mean field
  \[ X_n = C \sum_{\ell=1}^{N'} e^{-\gamma \ell} \left( x_n^{(j-\ell)} + x_n^{(j+\ell)} \right) \]

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

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

- normalization condition

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

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


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

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

• ordered product of the jacobian matrices

$$\tau_n = T_{n-1} T_{n-2} \cdots T_1 T_0, \quad T_n^{(ij)} = \frac{\partial x_n^{(i)}}{\partial x_n^{(j)}},$$

• for the chemical coupling in one spatial dimension

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

• where $r_{ij} = \min_\ell |i - j + \ell N|$
Lyapunov spectrum of coupled Bernoulli maps

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

- \( f(x) = \beta x \mod 1 \), strongly chaotic for \( \beta > 1 \)
- Lyapunov spectrum
  \[
  \lambda_k = \ln \beta + \ln \left| (1 - \varepsilon) + \frac{\varepsilon}{\kappa(\gamma)} b_k \right|
  \]
- 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


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

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

- \( \lambda_U \): 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

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

\[
\varepsilon_c = \frac{1}{2\Delta}, \quad \varepsilon'_c = \frac{3}{2\Delta'}
\]

\[
\Delta = 1 - \frac{b_1}{\kappa(\gamma)}, \quad \Delta' = 1 - \frac{b_{N'}}{\kappa(\gamma)}
\]
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 $\gamma$.
- 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 → adiabatic approximation no longer holds!

• Kuramoto model for chemical coupling can be generalized for time-dependent interaction kernels


• we can include motion of the oscillators → three timescales (oscillator, diffusion and motion): “active molecular dynamics” → challenges for computer simulations

• chemotaxis: oscillator motion depends on chemotactic forces, which are proportional to the local gradient of the concentration $\nabla A(r, t)$
Thank you very much