

# Collective modes of coupled phase oscillators with delayed coupling

Saúl Ares<sup>\*†</sup>, Luis G. Morelli<sup>†‡¶</sup>, David J. Jörg, Andrew C. Oates<sup>‡</sup>, and Frank Jülicher  
*Max Planck Institute for the Physics of Complex Systems*  
*Nöthnitzer Str. 38, 01187 Dresden, Germany*

We study the effects of delayed coupling on timing and pattern formation in spatially extended systems of dynamic oscillators. Starting from a discrete lattice of coupled oscillators, we derive a generic continuum theory for collective modes of long wavelength<sup>1</sup>.

The discrete lattice of coupled oscillators can be described by an evolution equation for the phase  $\theta_{\mathbf{i}}$  of the oscillator  $\mathbf{i}$ , coupled to its nearest neighbors  $\mathbf{j}$ :

$$\frac{d\theta_{\mathbf{i}}(t)}{dt} = \omega_{\mathbf{i}} + \frac{\varepsilon_{\mathbf{i}}}{2d} \sum_{|\mathbf{j}-\mathbf{i}|=1} h(\theta_{\mathbf{j}}(t-\tau) - \theta_{\mathbf{i}}(t)), \quad (1)$$

where  $\omega_{\mathbf{i}}$  is the intrinsic frequency of the oscillator  $\mathbf{i}$ ,  $\varepsilon_{\mathbf{i}}$  denotes the coupling strength of this oscillator to its neighbors, and  $\tau > 0$  is a time delay in the coupling. The coupling is described by the  $2\pi$ -periodic function  $h$ . Introducing the continuum phase  $\theta(x, t)$  and functions  $\omega(x)$  and  $\varepsilon(x)$  we show that the collective modes of long wavelength of Eq. (1) can be described by:

$$\begin{aligned} \frac{\partial\theta(x, t)}{\partial t} &= \omega(x) + \varepsilon(x)h(\theta(x, t-\tau) - \theta(x, t)) \quad (2) \\ &+ \frac{\varepsilon(x)a^2}{2}h''(\theta(x, t-\tau) - \theta(x, t)) \left( \frac{\partial\theta(x, t-\tau)}{\partial x} \right)^2 \\ &+ \frac{\varepsilon(x)a^2}{2}h'(\theta(x, t-\tau) - \theta(x, t)) \frac{\partial^2\theta(x, t-\tau)}{\partial x^2}, \end{aligned}$$

where the prime denotes the derivative of  $h$  with respect to its argument.

We use this approach to study spatial phase profiles of cellular oscillators in the segmentation clock, a dynamic patterning system of vertebrate embryos<sup>2,3</sup>. Collective wave patterns result from the interplay of coupling delays and moving boundary conditions<sup>4,5</sup>. We show that the phase profiles of collective modes depend on coupling delays, and derive experimental features of the segmentation clock starting from a very general framework.

---

\* saul.ares@csic.es Also member of Grupo Interdisciplinar de Sistemas Complejos (GISC). Present address: Logic of Genomic Systems Laboratory, Centro Nacional de Biotecnología - CSIC. Calle Darwin 3, 28049 Madrid, Spain.

† These authors contributed equally to this work.

‡ Max Planck Institute of Molecular Cell Biology and Genetics, Pfotenhauerstr. 108, 01307 Dresden, Germany.

¶ CONICET, Departamento de Física, UBA, Ciudad Universitaria, 1428 Buenos Aires, Argentina.

<sup>1</sup> S. Ares, L.G. Morelli, D.J. Jörg, A.C. Oates and F. Jülicher, *Phys. Rev. Lett.* **108** 204101 (2012).

<sup>2</sup> D. Roellig, L.G. Morelli, S. Ares, F. Jülicher and A.C. Oates, *Cell* **145**, 800 (2011).

<sup>3</sup> A.C. Oates, L.G. Morelli and S. Ares, *Development* **139**, 625 (2012).

<sup>4</sup> L.G. Morelli, S. Ares, L. Herrgen, C. Schröter, F. Jülicher and A.C. Oates, *HFSP J.* **3**, 55 (2009).

<sup>5</sup> L. Herrgen, S. Ares, L.G. Morelli, C. Schröter, F. Jülicher and A.C. Oates, *Curr. Biol.* **20**, 1244 (2010).