

# Coupling with delay: collective processes control period and pattern in vertebrate segmentation

Saúl Ares\*, Luis G. Morelli, Leah Herrgen, Christian Schröter, Frank Jülicher y Andrew C. Oates  
*Max Planck Institute for the Physics of Complex Systems*  
*Nöthnitzer Str. 38, 01187 Dresden, Germany*

We describe the dynamic patterns of gene expression<sup>1</sup> observed in vertebrate segmentation<sup>2</sup> (see Figure 1) using coupled phase oscillators<sup>3,4</sup>.

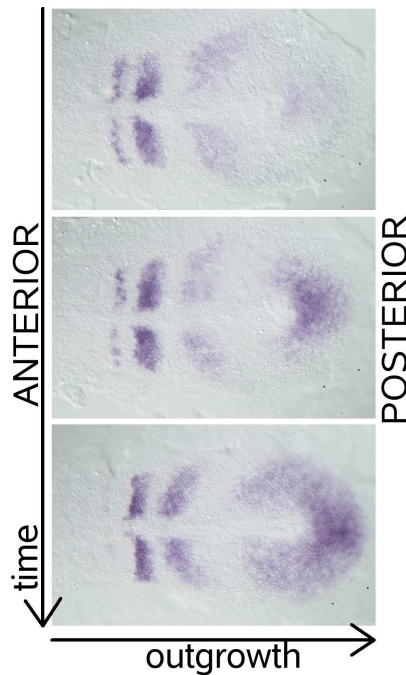


Figure 1. *In situ* experiments showing expression of the gene DeltaC mRNA in the Zebrafish pre-somitic mesoderm (PSM) of three different embryos, in sequential stages of development from up to down. The evolution of the wave pattern is the footprint of the oscillation in the expression of the gene.

Based on experimental evidence our description (Figure 2) introduces a frequency profile<sup>5</sup>, a moving boundary that describes axis elongation<sup>6</sup>, and coupling between neighboring cells, necessary to counteract the effect of noise and fluctuations<sup>7</sup>. To account for the time it takes for signaling molecules to be produced and exported to the cell membrane we include a time delay in the coupling. We derive analytical expressions for the phase profile, the wavelength of the patterns and the period of oscillations, and use them to determine segmentation pa-

rameters from available data. Together with experimental observations, our theory provides means to identify the role of genes involved in the segmentation of vertebrates. Our main finding is that the period of the segmentation clock is set by a collective process, strongly dependent on the characteristics of intercellular communication.

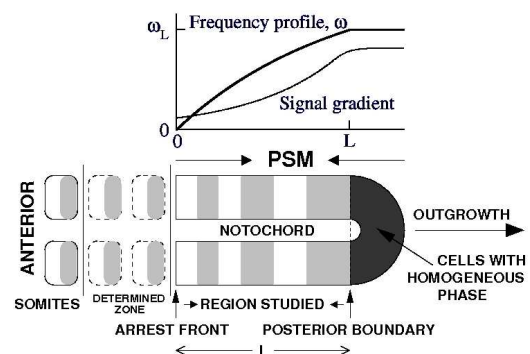


Figure 2. Diagram explaining the system under study. At the arrest front, the boundary condition imposed is the absence of phase diffusion across the boundary. At the posterior, it is the smooth coupling with the cells in the posteriormost shaded region. The signal gradient depicted (possibly related to FGF8 or Wnt gradients) is just a cartoon, the shape of this gradient is unknown.

\* saul@mpipks-dresden.mpg.de

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<sup>5</sup> J. Dubrulle, M.J. McGrew, and O. Pourquié, *Cell* **106**, 219-232 (2001).

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