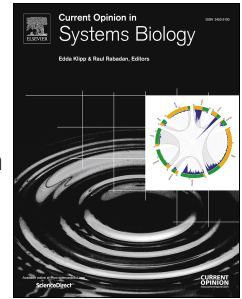


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Johannes Jaeger



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# Shift happens: the developmental and evolutionary dynamics of the gap gene system

Johannes Jaeger<sup>1-6\*</sup>

## Affiliations:

<sup>1</sup> EMBL/CRG Systems Biology Research Unit, Centre for Genomic Regulation (CRG), The Barcelona Institute of Science and Technology (BIST), Barcelona, Spain

<sup>2</sup> Universitat Pompeu Fabra (UPF), Barcelona, Spain

<sup>3</sup> Konrad Lorenz Institute for Evolution & Cognition Research (KLI), Klosterneuburg, Austria

<sup>4</sup> Complexity Science Hub (CSH), Vienna, Austria

<sup>5</sup> Center for Systems Biology Dresden (CSBD), Dresden, Germany

<sup>6</sup> Department for Molecular Evolution & Development, University of Vienna, Vienna, Austria

\* Corresponding author:

Johannes Jaeger, yoginho@gmail.com; current address: Complexity Science Hub (CSH) Vienna, Josefstädter Straße 39, 1080 Vienna, Austria

## Abstract

I review a systematic and quantitative comparative study of patterning by the gap gene network during early development in dipteran insects (flies and midges). This work demonstrates the use of reverse-engineering for integrating empirical data with mathematical modeling in order to reconstitute an evolving developmental process *in silico*. The resulting dynamical models (called gap gene circuits) provide necessary and sufficient mechanistic explanations for pattern formation by this system, and for its compensatory evolution by developmental system drift. Although not structurally modular, I show how the network can be decomposed into overlapping dynamical modules that exhibit differential sensitivity to evolutionary change, explaining the evolvability of the gap gene system.

## Introduction

The quest to understand the dynamics and the evolution of development is as old as biology itself. It remains one of the central challenges in our field. In recent years, it has become popular to characterize developmental processes that generate morphological traits using static graph representations of gene regulatory networks [1–4]. Evolvability—the capacity to produce adaptive change—is widely believed to require a modular network structure. Different approaches have been developed to identify and isolate structural modules, small network motifs or sub-circuits, that function and evolve with a certain

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