Variation and canalization of gene expression in the *Drosophila* blastoderm

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Development is surprisingly robust to environmental, genetic and stochastic variation. The widespread variation affecting morphogenic pathways exists in nature, but is usually silent due to buffering mechanisms. To formalize the concept of developmental stability against genetic and environmental perturbation C.H. Waddington presented his now famous "epigenetic landscape" and "canalization"(Waddington, 1940). The further development of Waddington's concepts is of great importance because it provides a scientific connection between the reliability and invariance of the formation of cell types and tissues in the face of underlying molecular variability. The morphogenetic field controlling segmentation in fruit fly *Drosophila* is a suitable model to address these problems due to a thorough characterization of this field at both molecular and genetics levels (Ingham, 1988; Surkova et al., 2008).

A particularly important class of phenomena concerns variation in the location of expression domain boundaries, as the segmentation gene cascade defines the boundaries of *wg* and *en* expression, that in turn define the parasegment boundaries. We showed that the positions of these boundaries are highly variable, when the expression domains form, and that this variation is dynamically reduced, or canalized, over time (Surkova et al., 2008).

Here we have used the gene circuit method to investigate the variance reduction phenomena in detail. We showed that the canalization of extensive variation in early gap gene expression patterns occurs by gap gene cross regulation. To explore how the canalization arises we undertook the analysis of the gap gene border formation in the model in terms of the phase portrait of the dynamical system. We demonstrated that the variation reduction of gap gene expression patterns is a consequence of the action of robust attracting states. We further showed that the complex patterning of the gap gene system reduces to the three qualitative dynamical mechanisms of (1) movement of attractors, (2) selection of attractors, and (3) selection of states on a one dimensional manifold. The last of the three mechanisms also causes the domain shifts of the gap genes, providing a simple geometric explanation of a transient phenomenon.