Emergence of Spatial Organization in Real Systems and its Modelling

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Patterns due to chemical instability is believed to be of essential importance in many biophysical systems, ranging from developmental biology [14], tumour metastases [3], controlled cell migrations (e.g. lung morphogenesis [15]), heterogeneous cell fate decision (nodal-lefty gene products [17], patterning in Drosophilla wing [2]), formation of skin patterns (mammalian coat markings or feather bud arrangements [16], Zebrafish mesodermal pigmentation [21, 11] to chemical reactions [1], vegetation stripes in landscape [20] or spatial patterns in mussel beds [23].

Systematic description of self-organisation in nature started by Turing [22] (mathematics) and also by Prigogine [18] (non-equilibrium thermodynamics). Typically, diffusion-driven instability (or Turing instability, TI) [22] is considered as the symmetry breaking mechanism. Turing showed that small local spatial fluctuations in an otherwise well-mixed system of autocatalytic and inhibitory diffusing species could become unstable due to diffusion and that an amplification of these fluctuations could lead to pattern development. Specifically, heterogeneous concentrations of chemicals form a 'pre-pattern'. Subsequent differentiation of tissue/cell type is in response to whether or not one of these morphogens exceeds some threshold locally.

The proposed TI mechanism, however, has several well-known limitations: sensitivity to noise (in initial conditions and to noise itself), Turing morphogens are hard to find (a possible Turing pair is Nodal/Lefty in zebrafish mesodermal induction) and that diffusion coefficients are significantly different as diffusion tends to smooth out local excess or the depletion of species but on the other hand, it can allow species to grow locally if this process occurs on different time-scales in the two species. However, as putative Turing pairs have similar molecular weights, this condition on the ratio of diffusion coefficient is in contrast to the Stokes-Einstein equation that relates diffusion constant to effective radius of a given molecule and to properties of the environment.

Turing model is successful in reproducing spatial organisation through a simple mechanism. Can we, however, infer its relevance to spatial organisation in real systems based on this feature? Probably the most limiting condition for TI is the need for significantly distinct diffusion constants. This condition can be rather naturally overcome by an approach set up by Lengyel-Epstein when activator binds to a substrate [12, 13]. Does this improve the relevance and plausibility of Turing mechanism to spatial organization in real systems? We shall argue that quite the contrary is true - it points to the problem of *reductionism*. These arguments led us to questioning the concept of TI leading to pattern formation itself in not well-controlled (e.g. biological) systems [8].

Is there some other framework able to describe spatial organisation and what about its relevance to real systems? We shall address both these questions by introducing the concept of non-equilibrium thermodynamics [5–7, 19] and apply it to Belousov-Zhabotinskii reactions offering a possible explanation [9, 10] of the recently observed phenomena of "revival" oscillations in Belousov-Zhabotinskii gels by mechanical stimulation [4].

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