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Generic oscillation patterns of the developing systems and their role in the origin and evolution of ontogeny

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ABSTRACT

The role of generic oscillation patterns in embryonic development on a macroscopic scale is discussed in terms of active shell model. These self-oscillations include periodic changes in both the mean shape of the shell surface and its spatial variance. They lead to origination of a universal oscillatory contour in the form of a non-linear dependence of the average rudiment's curvature upon the curvature variance. The alternation of high and low levels of the variance makes it possible to pursue the developmental dynamics irrespective to the spatiotemporal order of development and characters subject to selection and genetic control. Spatially homogeneous and heterogeneous states can alternate in both time and space being the parametric modifications of the same self-organization dynamics, which is a precondition of transforming of the oscillations into spatial differences between the parts of the embryo and then into successive stages of their formation. This process can be explained as a "retrograde developmental evolution", which means the late evolutionary appearance of the earlier developmental stages. The developing system progressively retreats from the initial self-organization threshold replacing the self-oscillatory dynamics by a linear succession of stages in which the earlier developmental stages appear in the evolution after the later ones. It follows that ontogeny is neither the cause, nor the effect of phylogeny: the phenotype development can be subject to directional change under the constancy of the phenotype itself and, vice versa, the developmental evolution can generate new phenotypes in the absence of the external environmental trends of their evolution.

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1. Introduction

A hypothesis that ontogenesis originates from self-organization (Goodwin, 1994; Cherdantsev et al., 1996; Beloussov, 1998, 2012) means that structuring is an egoistic process comparable to originating of the new self-reproduction modes at the intra-individual level having neither adaptive value nor inheritance on a scale of the organism. The only way in which self-organization can refer to evolution is in that the increase in complexity of the structural patterns generates in the developing system new variation canals and, consequently, evolutionary trends which persist irrespective of any change in specific directions of selection. By definition, the developing system arising from self-organization has no developmental history, which is certainly not the case for any extant developing organism. It follows, if we assume the self-organization hypothesis, that what we call the developmental history of a structure arises *after* the structure has emerged (Cherdantsev et al., 1996).

In dominating view, self-organization is a matter of reaction-diffusing systems (Turing, 1952; Meinhardt, 1982). The inconsistence of the theory is quite evident, because of the "interpretation problem" (Beloussov, 1998). Cells should know what the "local activators" and "distant inhibitors" mean, but how can they do that before selection has taught them to interpret concentrations of these substances? In his ingenious work, Turing (1952) emphasized that the point of self-organization is in that characters, which in the initial state could be actualized everywhere in the system, become restricted to only a part of this system. This is the only way in which a part of the system — *but not the characters of this part* — becomes a new structural domain. The only feasible connection with developmental evolution consists in the origination of a domain separation boundary and, consequently, new variation canal emerging on a macroscopic scale. The developing system becomes susceptible to changes that shift the domain-separation boundary irrespectively to the interpretation of characters that distinguish the domain from its surrounding.

It follows from this that self-organization is not compatible with a mainstream thesis of developmental biology that cells appreciate their positions in the developing system with no respect to its

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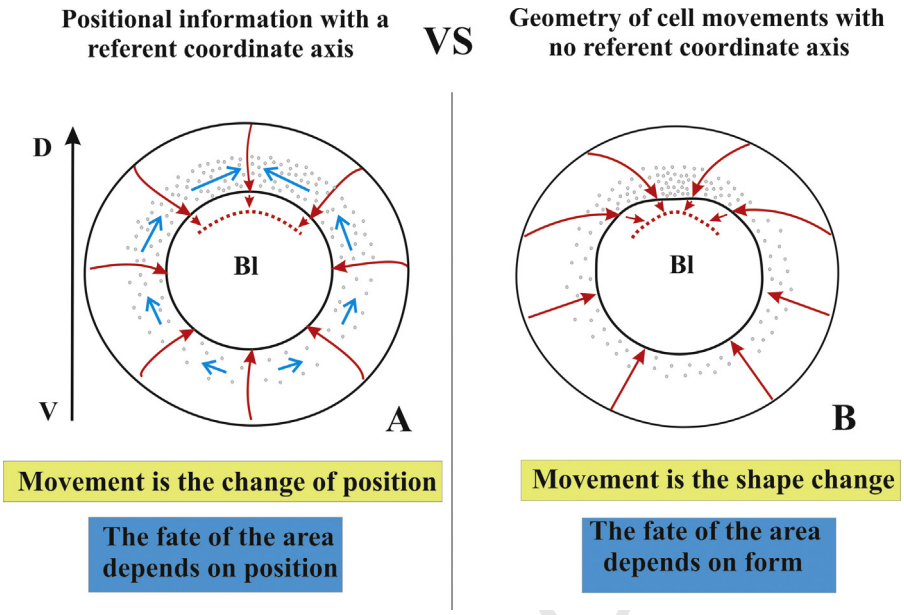

Fig. 1. Scheme illustrating two opposite approaches to morphogenesis, one basing on assigning of the cell positions in a referent coordinate system (A), and the other basing on the geometry of mass cell movements (B). DV – conventional dorsoventral axis of the embryo, Bl – blastopore, red arrows – cell movements toward the blastopore boundary, blue arrows – cell movements toward the blastopore dorsal pole, red dotted lines – the dorsal blastopore lip contour, dots – local cell concentrations.

geometry (Wolpert, 1969; De Robertis, 2006). The true seems to be converse (Cherdantsev, 2006): cells may have different positions because, and only because, the shape of the embryo is not uniform. The behavior of a cell seems to depend on its position only in an extent in which the form and, consequently, morphogenetic potencies of a given area differ from that of neighboring areas. Paradoxically, the closest to self-organization was an ancient concept of mosaic development considered the embryo as a mosaic of fragments, not in the sense of their early commitment but, rather, in the sense that their commitment, in its initial form, was not a stepwise hierarchical process taking place in the same referent coordinate system.

To illustrate this point, compare two manners of matching of the parts of the embryo to their positions taking as an example the idealized gastrulation in Chordates (Fig. 1). If we assume that the initial shape is uniform (in particular, at the initiation of gastrulation the blastopore boundary has a uniform curvature), then we get a scheme of gastrulation movements shown in Fig. 1A. In the absence of geometric differences, values of the cell movement vectors can differ only because of different positions of cells with respect to an axis conventionally denoted as the *DV* (dorsoventral) axis of the embryo. The initial symmetry provides two mass cell flows, one (big red arrows) directed to the blastopore boundary, and the other (blue arrows) directed along the blastopore boundary to the dorsal pole. These flows do not interact having, instead, a common dependence on the *DV* polarity. The local concentration of cells (shown by dots) increases at the dorsal and decreases at the ventral side with no change in the blastopore shape, except the blastopore closer. The outlined model inspired by modern versions of the positional information theory (see, for example, De Robertis, 2006) easily dispenses with morphogenesis and even physical forces.

In the geometric model, inferred from studies of gastrulation in amphibian (Cherdantsev, 2006; Scobeyeva, 2006) and teleost (Cherdantseva and Cherdantsev, 2006) embryos the initial shape is not uniform, the curvature of the dorsal blastopore boundary being smaller than that of the ventral one (Fig. 1B). Therefore, there is no need in referent coordinate axes because the *DV* polarity is a natural consequence of the geometric differences. The point is that one cannot inscribe the blastopore boundary into a single circumference and the consequences of this simple fact are mighty. First, local shape differences predict and explain shaping trends – this basic idea was first stated by Gurwitsch (1914) almost exactly a hundred years ago. The form itself provides a vector field to change this form, as shown in Fig. 1B by the small red arrows converting the dorsal blastopore boundary into the dorsal blastopore lip. Note that this is not the case in Fig. 1A where the small red arrows have a normal orientation with respect to the dorsal blastopore boundary. Second, the system tending to inscribe the unequal parts into a single circumference becomes subject to mechanical stress opening doors to the interplay of active and passive mechanical forces (Beloussov, 2012). Third, the dependence on geometry leads to a decrease in the number of variables being necessary for a description of the dynamics. Bending of the cell flows toward the region with a minimal curvature of the blastopore boundary shown in Fig. 1B by the big red arrows converts the two-parametric system of cell flows shown in Fig. 1A into one-parametric one.

Not denying and even emphasizing that the developing systems close to those shown in Fig. 1A do exist, there is a good likelihood to consider that, in the evolutionary view, these are secondary systems evolved from the systems shown in Fig. 1B. This hypothesis means, first, that the so-called primary embryonic axes have evolved from a mosaic of areas in which the shape differences among the areas were of more importance than the areas themselves including their positions. Then the hierarchical commitment of the embryonic rudiments is also a secondary phenomenon originating from inserting of the additional (intermediate) stages of their formation. Second, what we call the developmental stages could have evolved from self-oscillations by turning of the initially alternative states of embryonic areas into successive developmental stages of the whole embryo. In Fig. 1B, the ventral counterpart is subject only to a secondary shaping adjusting in to that of the dorsal counterpart. Then, in the evolutionary course, its formation, shifting to an earlier stage of the development and extending to the overall blastopore boundary, becomes a new stage of the dorsoventral differentiation.

Earlier we have shown that, in order to get both a separation of new structural domains and oscillatory dynamics it is sufficient to have a single geometric variable being an analog of the inhibitor in reaction-diffusion systems, while its spatial variance works like the activator of morphogenesis (Cherdantsev and Grigorieva,

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