

Pattern Formation on Skin of Fishes

by

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Introduction

Some animals have striped pattern on their skin, exemplified by zebra or tiger's coating. The developmental pattern formation of animal coating has been studied mathematically by a pair of partial differential equations, named a reaction-diffusion model of Turing type (2). In a typical model, the two substances are an activator and an inhibitor, and they follow local dynamics described by a pair of ordinary differential equations (3,4). The activator concentration enhances its own production rate and also promotes the production of the inhibitor, whilst the inhibitor concentration suppresses both activator and inhibitor. They also follow diffusion but the diffusion coefficient of the inhibitor is much larger than that of the activator. Without diffusion, the local dynamics of the two substances are stable and converging to the equilibrium. However with diffusion, the uniform distribution of both substances with concentrations equal to the equilibrium is unstable. Starting from an initial distribution very close to uniformity, a spatial heterogeneity emerges and a stable periodic pattern is formed spontaneously. Since this simple mechanism suggests that reaction of a small number of chemicals and their random diffusion might create stable nonuniform patterns. This mechanism was pointed out by Turing (3), for the first time in a one-dimensional space. When we analyze the model in a two dimensional plane, striped patterns in addition to spotted patterns often emerge. This was considered as the basic mechanism explaining many examples of stripe patterns observed among animal coating (2).

Meinhardt (4) has been developed many examples of pattern formation in development that can be explained by reaction-diffusion model. He often used a specific model, called "Gierer-Meinhardt" model, which was first proposed to explain the stable regeneration and pattern formation of hydras (5). There are other examples of reaction-diffusion models for Turing mechanism, such as Brusselator studied by a group of Belgium biophysicists (6) or Schnackenberg's (7), in which two substances are not an activator and an inhibitor. One substance has a larger diffusion coefficient than the other. The less diffusive substance tends to form clear stripe patterns and the more diffusive

substance mediates the interaction between neighboring areas with different concentration of the less diffusive substance.

Although patterns of mammal coating are quite suggestive of the involvement of reaction-diffusion models of Turing type, their pattern is formed during early stage of development, and the number of stripes is fixed through their life as the animal size grows. In contrast, the stripe patterns on fish skins, studied by Kondo and Asai (1), change their shape as the fish grows its body size. The number of stripes tends to increase with the body size but the width of each stripe and their distance between stripes remains almost unchanged. Kondo and Asai (1) studied the patterns of skins of several species of tropical fishes, and show that the change of their skin patterns can be explained very well by using a simple reaction-diffusion model of Turing type. Although the biological mechanism, including expression of responsible genes and the identity of activator and inhibitor, of the pattern formation of the fish stripes remains still unknown. However, the matching of the dynamical change in the stripe patterns with the fish body size and the prediction of the simple model is spectacular are strongly suggestive that stripe-patterns on fish skins depends on some spatial regulatory mechanism in a manner usefully modeled by reaction-diffusion model of Turing type.

In this study, we focus on the directionality of the stripes. Most of the stripes observed on fish skins are either parallel or perpendicular to their anterior-posterior (AP) axis, and the direction of the stripes is characteristic to each developmental stage and each species, although the pattern may change as the fish grows. For example, closely related pair of species in this genus (*Genicanthus melanosphilos* and *Genicanthus watanabei*) show different stripe patterns: *G. melanosphilos* shows has stripes perpendicular to AP axis and *G. watanabei* shows parallel stripe to the anterior-posterior axis. There are a few exceptions (e.g. stripes of random direction, oblique stripes).

The direction of stripes is considered of importance in the behavioral and ecological viewpoints -- in the case of African cichlid fishes, the vertical stripes tend to be associated with living in rocky substrate or vegetation, whilst the horizontal stripes are associated with schooling behavior (8).

On the other hand, all the reaction-diffusion models studied until now produce striped pattern without fixed directionality. Although the stripe patterns generated by the model in two-dimensional space has stable periodicity, the direction of the stripes is variable depending on the initial distribution if the domain to study is not very large. If the studied domain is large enough, the spatial pattern includes stripes in each local area but the direction of the stripe may differ between different parts of the domain. Hence these models are unable to explain the fixed directionality of stripes observed in many fish species.

In the present paper, we consider a modification of the basic reaction-diffusion model in a way to generate stripe patterns with a fixed direction. Fish skin is morphologically different along the antero-posterior axis and along the dorso-ventral axis. Figure 1 illustrates the structure of fish skin, showing cross-section along the AP axis. Scales are arranged in parallel to the AP-axis, and the epidermis is wrapping the scales and making a zigzag form. The melanocyte may be situated both in epidermis and in dermis, with the distribution differing between species. In zebrafish, a group of melanocytes are situated in epidermis (9). The zigzag structure doesn't exist along the dorso-ventral axis. Hence it is quite likely that the diffusion of substances or the strength of the interaction between neighboring sites, or the speed of transferring information can differ between along the AP-axis and along the DV-axis. This might create a difference in the diffusion speed in the direction along the two axes.

In the following, we study a reaction-diffusion model in which the substances can diffuse faster in a certain specific direction than other direction. Hence the diffusion of the two substances can be anisotropic (rather than isotropic). We show that the direction of both final and the transitional patterns in actual fish can be explained well by the model. The directions of the stripes depend on the difference in the magnitude in anisotropy between two substances, rather than their absolute magnitude of anisotropy. Only when the values of anisotropy are almost same between the two substances, the specificity of the stripe direction disappears. We discuss the biological significance of this result.

Model

The pattern observed on fish skin reflects the distribution of melanocytes in the epidermis. The biological mechanism to generate the spatially regular pattern is still unknown. We here assume that the spatio-temporal interaction of the activity in fish epidermis can be modeled by a reaction-diffusion system of two variables on two-dimensional space. Although the model is a pair of partial differential equations, it does not necessarily indicate the involvement of diffusive chemical substances, but these two variable represent the intensities of two processes -- one finally causing a higher melanocyte density whilst the other mediating interaction between neighboring areas of skin. We assume that the morphological anisotropy of fish skin causes the anisotropy in the diffusion. In the diffusion of a substance, the flux increases in proportional to the gradient of its concentration, with the proportionality coefficient equal to the diffusion coefficient. In the present study, the diffusion coefficient depends on the direction of the gradient vector.

The model is given as follows:

$$\frac{\partial u}{\partial t} = \nabla(D_u(\theta_u)\nabla u) + \gamma f(u, v), \quad \mathbf{[1a]}$$

$$\frac{\partial v}{\partial t} = d\nabla(D_v(\theta_v)\nabla v) + \gamma g(u, v), \quad \mathbf{[1b]}$$

where u and v are the concentration of two substances. $f(u, v)$ and $g(u, v)$ are the reaction terms. Here we rescale the space and time variables in a way in which the diffusion coefficient for u is 1. Reaction terms are multiplied by a rare constant γ , and the diffusion coefficient for v becomes the ratio of diffusion coefficient for the two substances. d is a constant larger than 1, which implies that v has a diffusion coefficient larger than u . If $D_u(\theta_u) = D_v(\theta_v) = 1$, the above model is the standard reaction-diffusion model. We call u and v "less-diffusive-substance" and "more-diffusive-substance," respectively. $D_u(\theta_u)$ and $D_v(\theta_v)$ are the functions for anisotropy and are given by

$$D_u(\theta_u) = \frac{1}{\sqrt{1 - \delta_u \cos 2\theta_u}}, \quad [2a]$$

$$D_v(\theta_v) = \frac{1}{\sqrt{1 - \delta_v \cos 2\theta_v}}, \quad [2b]$$

where θ_u and θ_v indicate the angles of the gradient of the variables ($\theta_u = \tan^{-1}\left(\frac{\partial u/\partial y}{\partial u/\partial x}\right)$ and $\theta_v = \tan^{-1}\left(\frac{\partial v/\partial y}{\partial v/\partial x}\right)$). We chose x -axis parallel to a specific direction (which may be the DV-axis) along which the diffusion of substances occur faster than the other directions. To indicate this, the diffusion coefficient of u is $D_u(\theta_u)$ and that of v is $D_v(\theta_v)$, both of which are largest when gradients (θ_u and θ_v , respectively) is parallel to the x -axis. δ_u and δ_v indicates the magnitude of anisotropy of two substances, and satisfy $0 \leq \delta_u < 1$ and $0 \leq \delta_v < 1$. We assumed that the flux is greater if the gradient vector of the substance was the same as the special direction (x -axis), and that it would be reduced if the direction of the gradient vector was perpendicular to the special direction. The modeling of anisotropic diffusion in a manner given by Eq. 2 was adopted by Kobayashi (10) who studied the pattern formation of the dendritic crystal growth such as snow crystals, but he used different function for $D_u(\theta_u)$ and $D_v(\theta_v)$ (explained later).

As the reaction terms, f and g , we first examined the case with the simplest choice proposed by Schnackenberg (7):

$$f(u, v) = A - u + u^2 v, \quad [3a]$$

$$g(u, v) = B - u^2 v, \quad [3b]$$

where A and B are positive constants. We also analyzed models with alternative choices of reaction terms, and we will explain them later.

The Equilibrium Patterns

We derived the spatial patterns formed after a long time calculation by computer

simulation of the model given by Eqs. 1-3. The parameter values used in the calculation are ones that generate stripes in simple reaction-diffusion model (when both δ_u and δ_v are 0). The initial distributions are close to the uniform distribution of u and v that are equal to the equilibrium of the ordinary differential equations with additional small random deviations. We used several initial distributions with different random deviations and confirmed the robustness of the result. To remove the effect of the boundary, the periodic boundary condition was adopted. The total number of calculation steps was about 8000, which was sufficiently large for the dynamics to reach the final static state. To remove the possibility that the directionality of stripes arise simply from the effect of the directionality of numerical analysis, we run simulations for cases with different methods of discretization, and obtained the same results.

(1) Both substances are equally anisotropic

First, we study the case in which the magnitude of anisotropy is the same between the two substances ($\delta_u = \delta_v > 0$). Figure 2 shows the simulation results. The directionality of the stripes is not observed, in spite that the diffusion occur faster along the x -axis than along the y -axis. The pattern looks quite similar to the one generated by the standard reaction-diffusion model with isotropic diffusion ($\delta_u = \delta_v = 0$). The absence of specific directionality of stripes holds even if the value of the anisotropy is very large. This result is understandable because if both substances are equally diffusive along the x -axis than along the y -axis, the system may simply be the same as the field is enlarged along the x -axis. Then just increasing or decreasing the diffusion speed to a direction does not make the direction of the stripes fixed.

(2) Only the less diffusive substance is anisotropic

Second, we incorporated the anisotropy only in the diffusion of the less diffusive substance u , and the less diffusive substance v follows isotropic diffusion. Figure 3 shows the simulation results when the anisotropy of u is positive and that of v is 0 ($\delta_u > 0$, $\delta_v = 0$). All the stripes were formed in parallel to the x -axis, which is the most diffusive

direction of u . The three patterns in Fig. 5 are for different magnitude of anisotropy of u . The directionality in the stripe pattern was clearer for a larger magnitude of anisotropy δ_u . On the other hand, the wave-length of the stripe is independent of the magnitude of anisotropy, δ_u .

(3) Only the more diffusive substance is anisotropic

Then we studied the opposite cases, in which the more diffusive substance v follows anisotropic diffusion, but the less diffusive substance u follows isotropic diffusion. Figure 4 shows the results when the anisotropy of v is positive and that of u is 0 ($\delta_u=0, \delta_v>0$). Now, the direction of the stripes is perpendicular to the x -axis which is the most diffusive direction of v .

(4) General cases

We have examined the stripe patterns for various combinations of the anisotropy of the two substances. Figure 5 summarizes the direction of stripes in the final spatial patterns calculated by the computer algorithm explained in Appendix A.

Figure 5 shows that the directionality of stripes depends only on the relative magnitude of anisotropy of u and v . When the δ_u is larger than δ_v , the direction of the stripe is horizontal, i.e. the direction of stripe is parallel to the most diffusive direction. When the δ_v is larger than δ_u , the direction of stripe is perpendicular to the most diffusive direction. Only when the anisotropies of both substances are almost the same, the direction of stripes was not determined.

We did the same analysis for the model with modified conditions -- with different value of parameters in reaction terms, with different ratio of two diffusion coefficients d , and with different functional forms of the diffusion anisotropy, but we obtained very similar results. For example, Fig. 6 shows the direction of stripes generated using an alternative diffusion coefficient function, explained in Appendix B, which is quite similar to Fig. 5. From these analysis we conclude that the direction of stripes depend on the relative magnitude of anisotropy of the two substances.

Dynamical Change of the Patterns

The model can explain not only the final pattern but also the transit patterns of fish skin. In *Genicanthus*, the stripe pattern appears during its sex change (not shown here). The fish initially has a plain skin without stripes and a clear stripe pattern appears as the individual change sex from female to male (11). Initially many spots of high concentration of u appeared, and then they became elongated and connected with each other, and finally the location of stripes shifted and making stripes without branching equally spaced with each other. This transition of events when stripes appear during the sex change period is exactly the one observed for the computer simulation of the model (Fig. 7).

Discussion

The results can be summarized as follows: when the anisotropy of the less diffusive substance is larger than that of the more diffusive one, stripes run parallel to the direction of the highest diffusivity. In contrast when the anisotropy of the more diffusive substance is larger than that of the less diffusive substance, stripes run perpendicular to the direction of the highest diffusivity. A small difference in diffusion anisotropy can produce the final pattern with a clear directionality. Only when the anisotropy's are almost the same between the two substances, the specificity of the stripe direction disappears. This result holds irrespective of the choice of the diffusion coefficient, parameters in the reaction terms, or the function of diffusion coefficients (see Appendix B).

We also examined the the reaction-diffusion models of Turing type in which reaction terms are not the Schanackenberg model, given by Eq. 3, but the Gierer-Meinhardt model and the linear model with truncation, which are explained in Appendix B. Figure 8 shows the direction of stripes generated by the Gierer-Meinhardt model, and it is

quite similar to Fig. 5. In any of these reaction-diffusion models with anisotropic diffusion of the two substances, the same conclusion can be obtained concerning the direction of stripes to be formed -- the stripes in the final spatial pattern are parallel to the specific direction with the highest diffusivity if the less diffusive substance has a stronger anisotropy than the more diffusive substances, whilst stripes perpendicular to the direction of the highest diffusivity are to be formed if the more diffusive substance is more strongly anisotropic than the less diffusive substances.

As the relative magnitude of anisotropy of the two substances changes continuously, we may observe abrupt change in the direction of stripes from the anterior-posterior axis to the dorsal-ventral axis. The model suggests that two closely related species might have a contrasting difference in the directionality of stripes on their skin.

Since the morphological structure of fish skin gives directionality along the anterior-posterior axis, the model concludes that the fish skin tends to have the stripes either along the anterior-posterior axis or along the dorso-ventral axis (perpendicular to the AP axis), but rarely having stripes of other direction, such as oblique directionality. This seems to be supported by the observations.

According to the model, the two substances must be different in anisotropy in order to generate the fixed directionality of stripes characteristics to each species. We expect that the way of the spatial transportation may be different between the pattern-generating factors in the fish skin. If the anisotropy of diffusion is caused by the morphological structure of the skin, it may be possible that there are two or more substances that are responsible for generating the stripe pattern of melanocytes diffuse in different layers of the fish skin. However, as we stated before, two "substances" in the model may not imply diffusive chemicals, but they represent two processes with different range of spatial interaction. The model's result that the two processes should have different anisotropy should be helpful in identifying the processes mediating the spatial interaction between neighboring areas of the fish skin, which are responsible for the formation of striped melanocyte distribution in the skin.

Appendix A

Quantifying the direction of the stripes in a given spatial pattern

Let $u(\mathbf{x})$ be the magnitude of u at location \mathbf{x} . To know whether a spatial pattern has stripes with a fixed direction and to quantify the direction to which stripes are formed, we define the spatial auto-correlation function.

$$I(r, \theta) = \frac{1}{A\sigma^2} \int \{u(\mathbf{x}) - \bar{u}\} \{u(\mathbf{x} + \mathbf{r}) - \bar{u}\} d\mathbf{x}, \quad [\text{A1}]$$

where $\mathbf{r} = \begin{pmatrix} r \cos \theta \\ r \sin \theta \end{pmatrix}$. \bar{u} and σ^2 are the mean and the variance of $u(\mathbf{x})$, defined as,

$$\bar{u} = \frac{1}{A} \int u(\mathbf{x}) d\mathbf{x}, \quad [\text{A2a}]$$

$$\sigma^2 = \frac{1}{A} \int \{u(\mathbf{x}) - \bar{u}\}^2 d\mathbf{x}. \quad [\text{A2b}]$$

where A is the total area of the region. $I(r, \theta)$ is the correlation between two sites separated by distance r and with the relative directional angle θ . To focus on the effect of relative directional angle θ , we calculated the average of $I(r, \theta)$ with respect to distance r from R_1 to R_2 , which were chosen to make the clearest result.

$$I_R(\theta) = \int_{R_2}^{R_1} I(r, \theta) dr. \quad [\text{A3}]$$

We chose R_1 a little less than half and R_2 a little more than twice of the distance between adjacent strips. Then we searched for the angle which attains the maximum of $I_R(\theta)$.

This specific direction is the maximum point in picking up the mode in the period. Let us denote this by ψ . If we calculate the Fourier series of $I_R(\theta)$:

$$I_R(\theta) \sim a + b \cos(2(\theta - \psi)) + [\text{other components}]. \quad [\text{A4}]$$

If the stripe pattern is clear, the second term should be much larger than all the other components. Hence we can obtain ψ by the same method to calculate the Fourier series:

$$\int_0^{2\pi} I_R(\theta) \cos 2\theta d\theta = b\pi \cos 2\psi \quad \text{and} \quad \int_0^{2\pi} I_R(\theta) \sin 2\theta d\theta = b\pi \sin 2\psi, \quad [\mathbf{A5}]$$

From the ratio of these, we can calculate ψ , the direction to which the stripes run. The amplitude b in this expression, also obtained by Fourier series, implies the importance of the component, or clearness of the stripe pattern.

Appendix B

Alternative functions of anisotropy:

In this paper, we mainly used the anisotropic diffusion coefficients given by Eq. 2. When Kobayashi (10) modeled the anisotropy in diffusion in his study of pattern formation of dendritic crystal growth, he adopted a function given as:

$$D_{\sigma}(\theta) = 1 + \delta_{\sigma} \cos 2\theta, \quad \sigma = u, \text{ and } v, \quad [\mathbf{B 1}]$$

which are different from Eq. 2. We have also carried out the analysis using Eq. B 1. The results are shown in Fig. 6, which is very similar to Fig. 5, suggesting the robustness of the results.

Alternative formulae of reaction terms:

In this paper, we mainly used the Schnackenberg model given by Eq. 3 for reaction terms. To show that the same results hold irrespective of the choice of reaction terms, we examined the two other models of reaction-diffusion of Turing type.

[1] The Gierer-Meinhardt model (4,5)

This model is the activator-inhibitor mechanism suggested by Meinhardt (4).

Their reaction terms are:

$$f(u, v) = A - Bu + \frac{u^2}{v}, \quad [\mathbf{B2a}]$$

$$g(u, v) = u^2 - v, \quad [\mathbf{B2b}]$$

where A and B are constants. In the computer simulation, we used $A = -0.14$, $B = 0.74$, and diffusion coefficient $d = 5.00$. The result is shown in Fig. 8. This result is again very similar to Fig. 5.

[2] The linear reaction model (5).

To discuss the growth related change in skin patterns for tropical fishes, Kondo and Asai (5) adopted the reaction-diffusion model with the following reaction terms:

$$f(u, v) = Au - v + C, \quad \text{[B3a]}$$

$$g(u, v) = Bu - v + 1. \quad \text{[B3b]}$$

where A , B , and C are constants. They also assume truncation to avoid unrealistic situations that densities of the substances diverge to infinity. In computer simulation we used $A = 0.90$, $B = 1.20$, $C = 0.16$, and relative diffusion coefficient $d = 5.00$. The result of this case (not shown here) was also very close to Fig. 9 or Fig. 5.

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Figure Legends

Figure 1 A schematic drawing of the morphological structure of fish skin, (modified and redirection from (12)).

Figure 2 The patterns obtained after long time calculation by computer simulation. Both the diffusive substance u and v diffuse in an anisotropic manner. The most diffusive direction is parallel to the x -axis. Parameters are $a=0.025$, $b=1.550$, $d=20$, $\gamma = 10000$. The boundary condition is periodic. The spatial size is 2.0×2.0 (grid : 200×200). a: $\delta_u = \delta_v = 0.05$. b: $\delta_u = \delta_v = 0.10$. c: $\delta_u = \delta_v = 0.50$.

Figure 3 The spatial patterns obtained by computer simulation. Only the less diffusive substances u diffuses in anisotropic way. The direction of the largest diffusive direction is parallel to the x -axis. The parameters are the same as in Fig. 2 except for δ_u and δ_v . The δ_v is zero, and δ_u is positive. a: $\delta_u = 0.05$. b: $\delta_u = 0.10$. c: $\delta_u = 0.50$.

Figure 4 The patterns obtained after a long time calculation by computer simulation. Only the more diffusive substance v diffuses in an anisotropic manner. The most diffusive direction is parallel to the x -axis. The parameters are the same as in Fig. 2 and 3 except for δ_u and δ_v . The δ_u is zero, and δ_v is positive. a: $\delta_v = 0.05$. b: $\delta_v = 0.10$. c: $\delta_v = 0.50$.

Figure 5 The summary of the direction of obtained stripe patterns. The direction was identified by using the method shown in Appendix A. The horizontal and vertical axis indicate δ_u and δ_v , respectively. Each point indicates the direction of the observed stripe, horizontal (\circ), vertical (\bullet), or not determined (\times). The direction is determined only by the difference between δ_u (horizontal axis) and δ_v (vertical axis). Parameters are: $a=0.025$, $b=1.550$, $\gamma = 10000$, and $d=20$.

Figure 6 The summary of the direction of obtained stripe patterns when we use alternative function of anisotropy studied by Kobayashi (10), which is shown in Appendix B.

Figure 7 Spatial patterns of model given by Eqs. **1-3** obtained in every 1600 time steps. Parameters are: $a=0.025$, $b=1.550$, $d=20$, $\delta_u=0.50$, $\gamma = 10000$. (a)-(e): $\delta_u=0.30$, $\delta_v=0.00$, and (f)-(j): $\delta_u=0.00$, $\delta_v=0.30$. The boundary condition is periodic. The spatial size is 2.0×2.0 (grid : 200×200).

Figure 8 The summary of the direction of obtained stripe patterns when we use different reaction term, which is studied by Gierer and Meinhardt (see Appendix B). Parameters are $A=-0.140$, $B= 0.740$, $\gamma = 10000$, and $d=5$.

Figure 1
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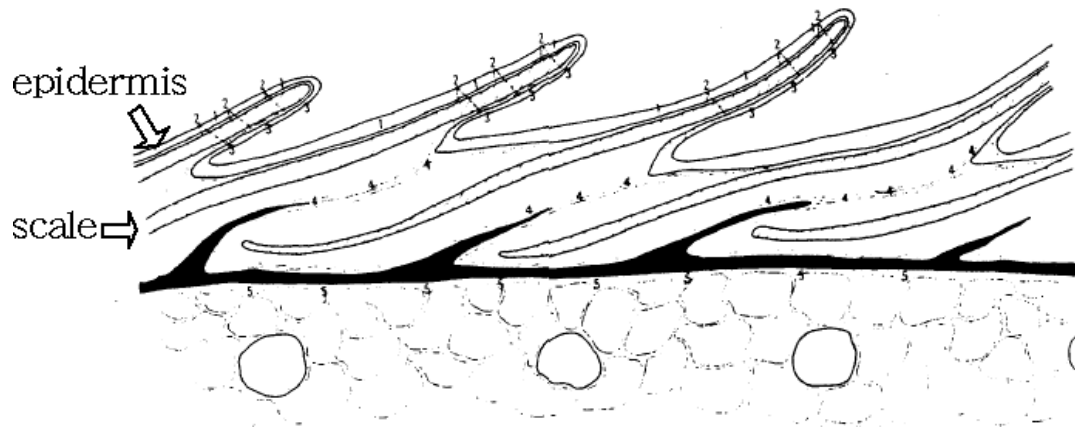


Figure 2
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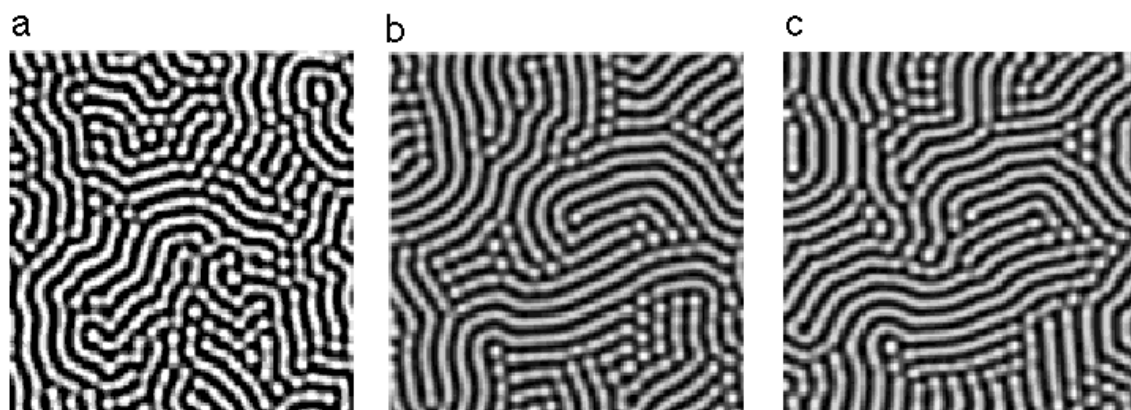


Figure 3
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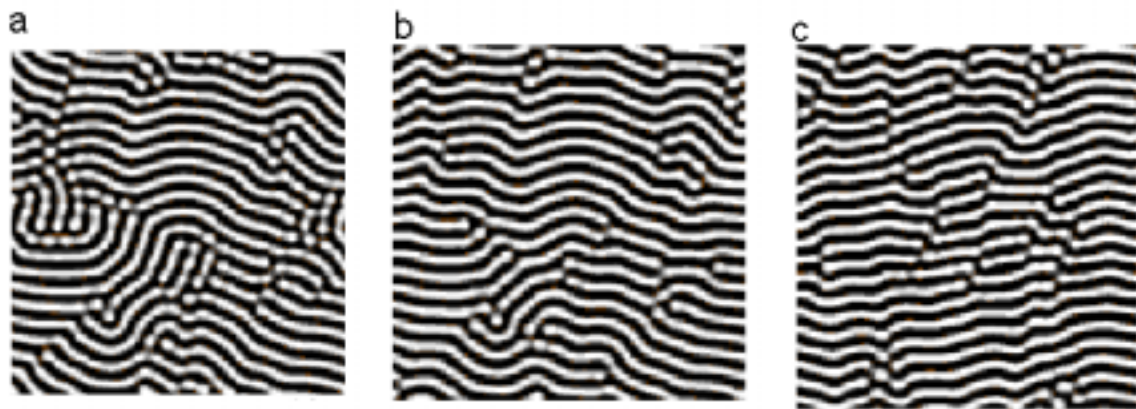
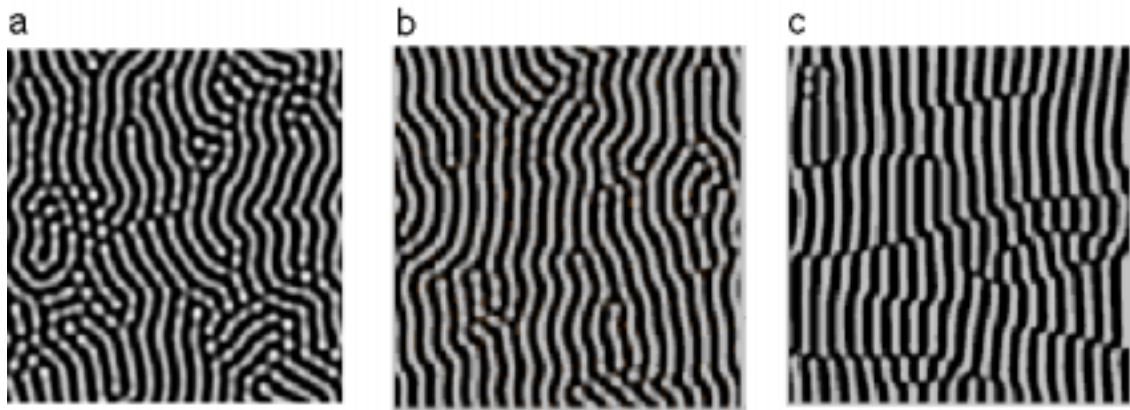


Figure 4
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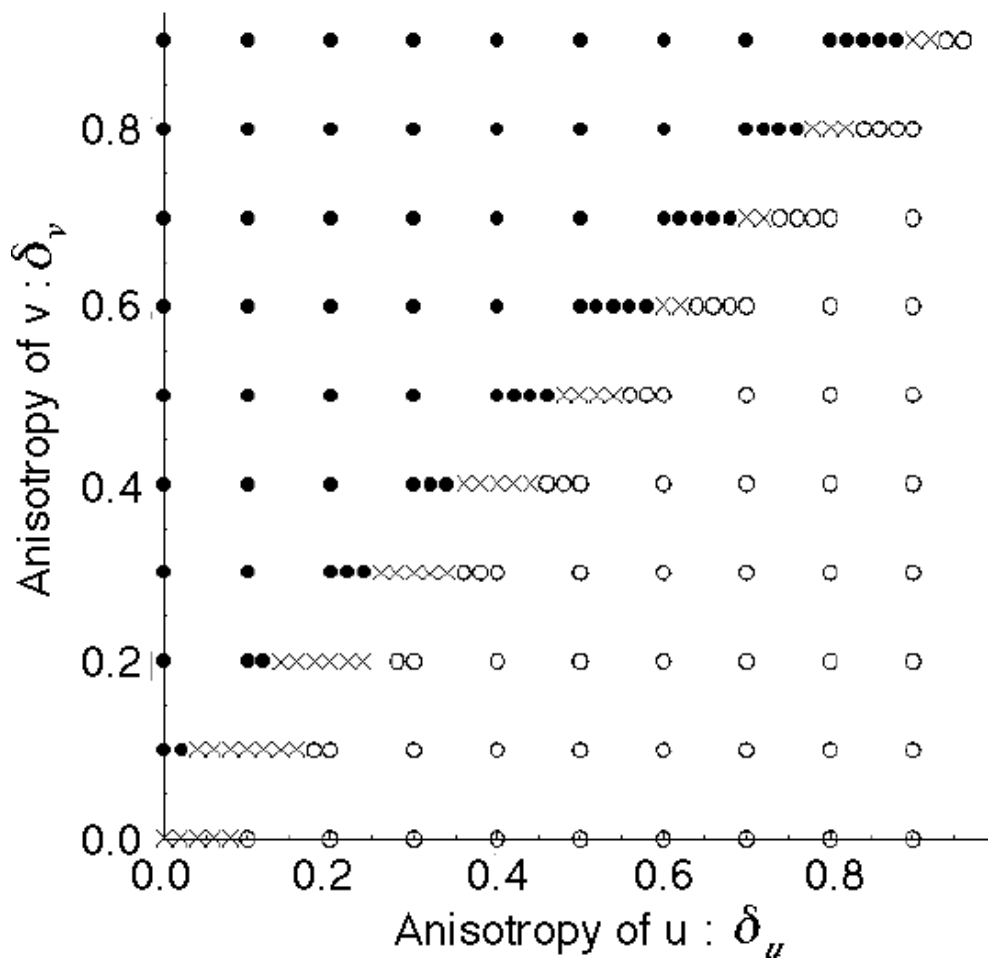


Figure 5
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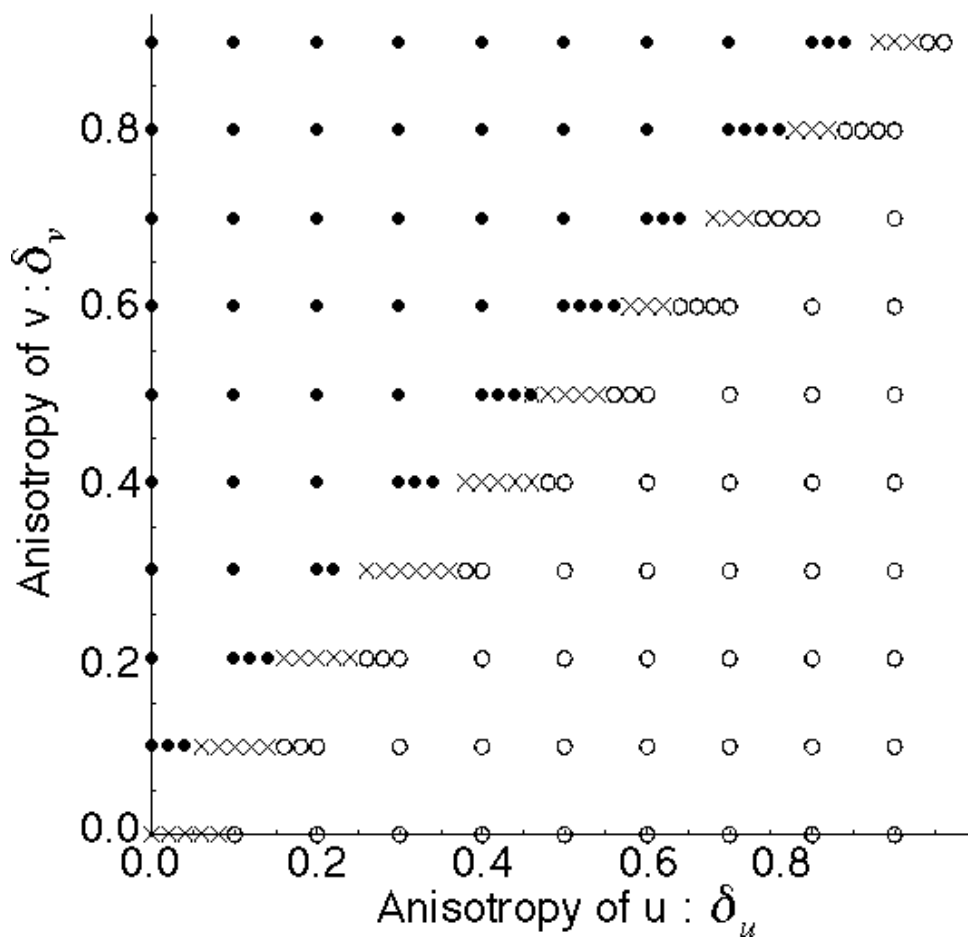
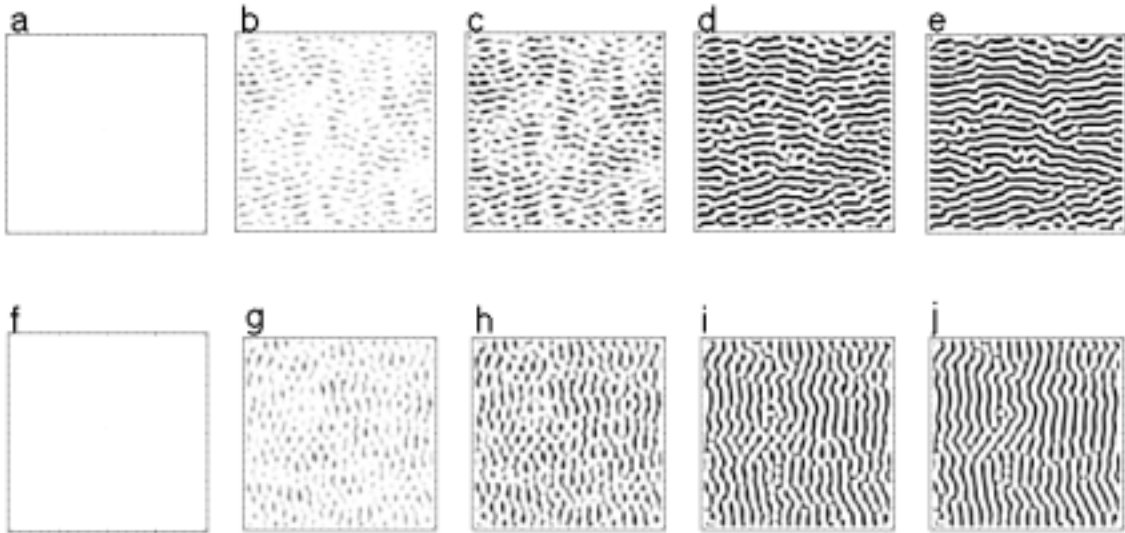


Figure 6
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Figure 7
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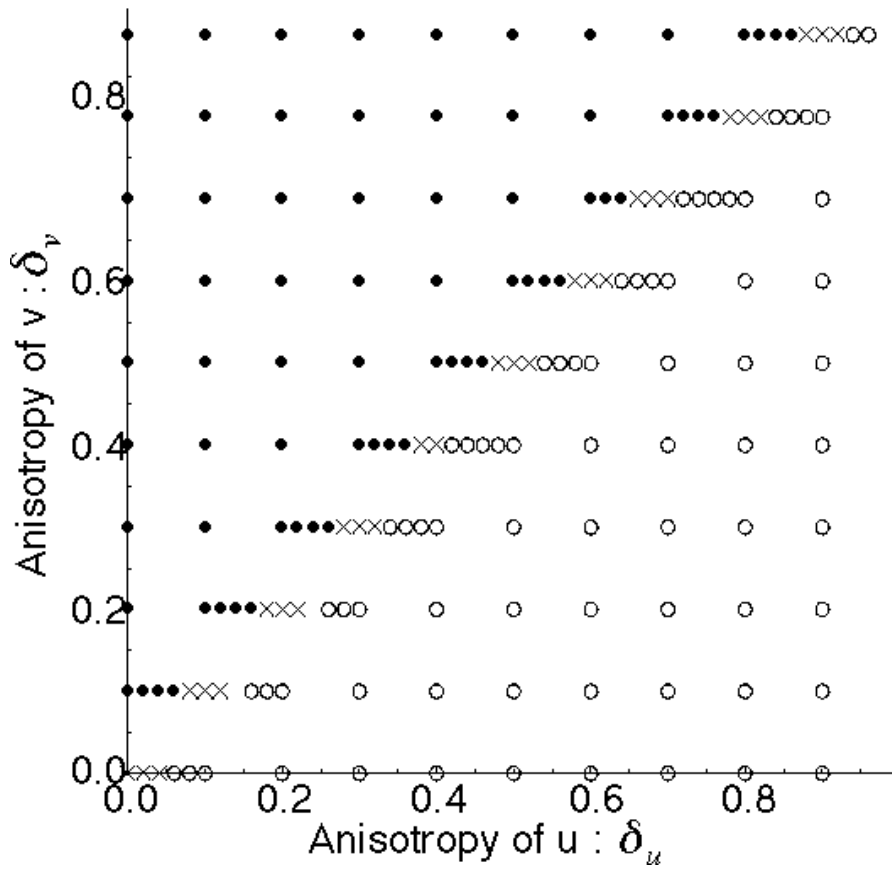


Figure 8
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