Pattern Formation - Homework 4 **Deadline: November 12, 6PM**

(1) **Morphogenesis** (40pt)

Let us consider the morphogenesis model described in the following pages. Determine the homogeneous stationary solution $a = a_0, h = h_0$ of the system. Find the values of the control parameters where the homogeneous solution loses its stability. What is the instability type and what kind of patterns do we expect to observe?

10.4 A Model for Morphogenesis

When reading our book the reader may have observed that each discipline has its "model" systems which are especially suited for the study of characteristic features. In the field of morphogenesis one of such "systems" is the hydra. Hydra is an animal a few mm in length, consisting of about 100,000 cells of about 15 different types. Along its length it is subdivided into different regions. At one end its "head" is located. Thus the animal has a "polar structure". A typical experiment which can be done with hydra is this: Remove part of the head region and transplant it to another part of the animal. Then, if the transplanted part is in a region close to the old head, *no* new head is formed, or, in other words, growth of a head is *inhibited*. On the other hand, if the transplant is made at a distance sufficiently far away from the old head, a new head is formed by an *activation* of cells of the hydra by the transplant. It is generally accepted that the agents causing biological processes such as morphogenesis are chemicals. Therefore, we are led to assume that there are at least two types of chemicals (or "reactants"): an *activator* and an *inhibitor*. Nowadays there is some evidence that these activator and inhibitor molecules really exist and what they possibly are. Now let us assume that both substances are produced in the head region of the hydra. Since inhibition was present still in some distance from the primary head, the inhibitor must be able to diffuse. Also the activator must be able to do so, otherwise it could not influence the neighboring cells of the transplant.

Let us try to formulate a mathematical model. We denote the concentration of the activator by a, that of the inhibitor by h. The basic features can be seen in the frame of a one-dimensional model. We thus let a and h depend on the coordinate x and time t. Consider the rate of change of a, $\partial a/\partial t$. This change is due to

1) generation by a source (head):

production rate: ρ, (10.21)

2) decay: $-\mu a$, (10.22)

where μ is the decay constant

3) diffusion: $D_a \frac{\partial^2 a}{\partial x^2}$, (10.23)

D_a diffusion constant.

Furthermore it is known from other biological systems (e.g., slime mold, compare Section 1.1) that autocatalytic processes ("stimulated emission") can take place. They can be described—depending on the process—by the production rate

$$k_1 a, \tag{10.24}$$

or

$$k_2 a^2, \text{ etc.} \tag{10.25}$$

Finally, the effect of inhibition has to be modelled. The most direct way the inhibitor can inhibit the action of the activator is by lowering the concentration of a. A possible "ansatz" for the inhibition rate could be

$$-ah. \tag{10.26}$$

Another way is to let h hinder the autocatalytic rates (10.24) or (10.25). The higher h, the lower the production rates (10.21) or (10.25). This leads us in the case (10.25) to

$$k \frac{a^2}{h}. \tag{10.27}$$

Apparently there is some arbitrariness in deriving the basic equations and a final decision can only be made by detailed chemical analysis. However, selecting typical terms, such as (10.21), (10.22), (10.23), (10.27), we obtain for the total rate of change of a

$$\frac{\partial a}{\partial t} = \rho + k \frac{a^2}{h} - \mu a + D_a \frac{\partial^2 a}{\partial x^2}. \tag{10.28}$$

Let us now turn to derive an equation for the inhibitor h. It certainly has a decay time, i.e., a loss rate

$$-vh, \tag{10.29}$$

and it can diffuse:

$$D_h \frac{\partial^2 h}{\partial x^2}. \tag{10.30}$$

Again we may think of various generation processes. Gierer and Meinhard, whose equations we present here, suggested (among other equations)

$$\text{production rate: } ca^2, \tag{10.31}$$

i.e., a generation by means of the activator. We then obtain

$$\frac{\partial h}{\partial t} = ca^2 - vh + D_h \frac{\partial^2 h}{\partial x^2}. \tag{10.32}$$

Before we represent our analytical results using the order parameter concept in Section 10.5, we exhibit some computer solutions whose results are not restricted to the hydra, but may be applied also to other phenomena of morphogenesis. We simply exhibit two typical results: In Fig. 10.2 the interplay between activator and inhibitor leads to a growing periodic structure. Fig. 10.3 shows a resulting two-dimensional pattern of activator concentration. Obviously, in both cases the inhibitor suppressed a second center (second head of hydra!) close to a first center (primary head of hydra!). To derive such patterns it is essential that h diffuses more easily than a, i.e , $D_h > D_a$. With somewhat further developed activator-inhibitor models, the structures of leaves, for example, can be mimicked.

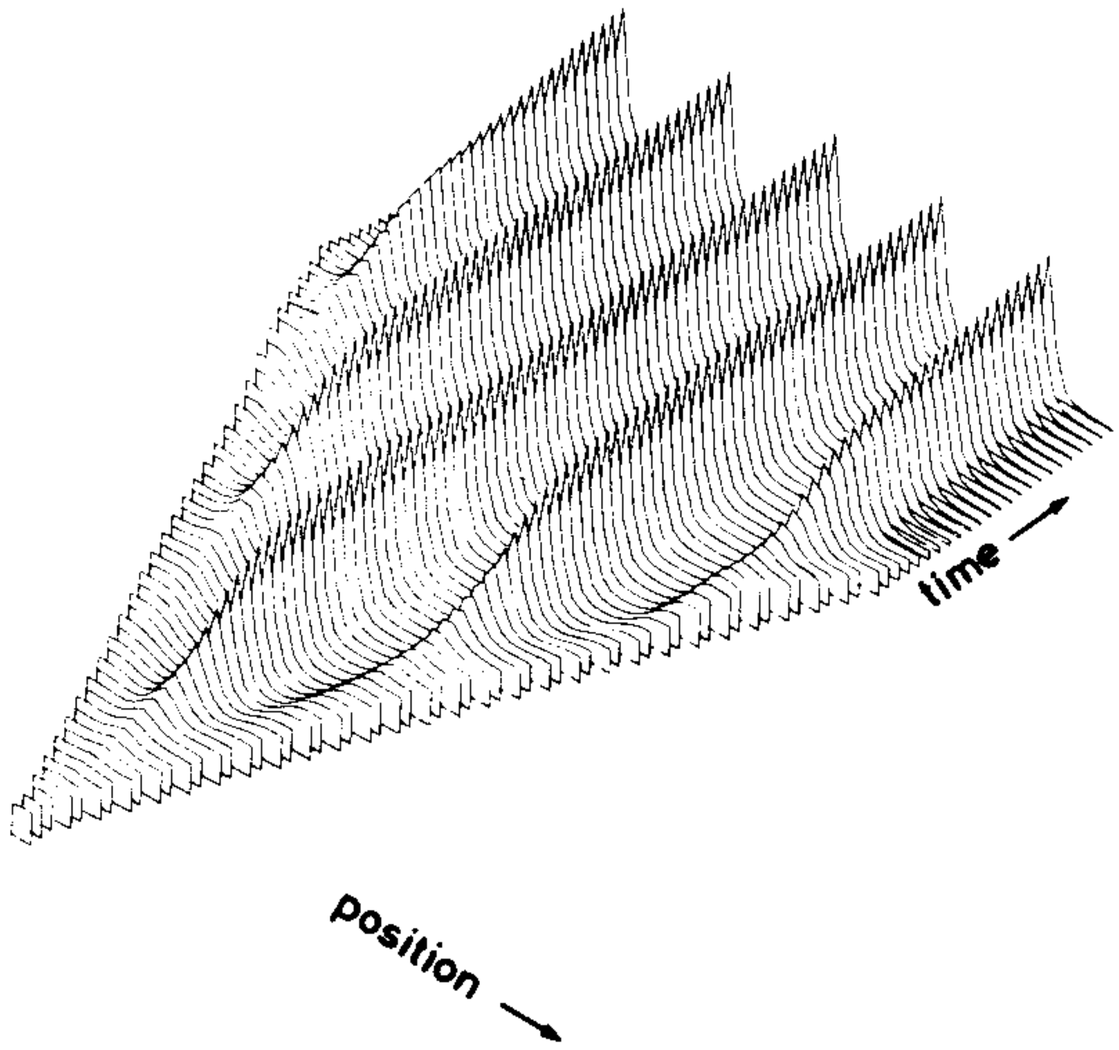

Fig. 10.2. Developing activator concentration as a function of space and time (computer solution). (After *H. Meinhardt, A. Gierer:* J. Cell Sci. **15**, 321 (1974))

In conclusion we mention an analogy which presumably is not accidental but reveals a general principle used by nature: The action of neural networks (e.g., the cerebral cortex) is again governed by the interplay between short-range activation and long-range inhibition but this time the activators and inhibitors are neurons.

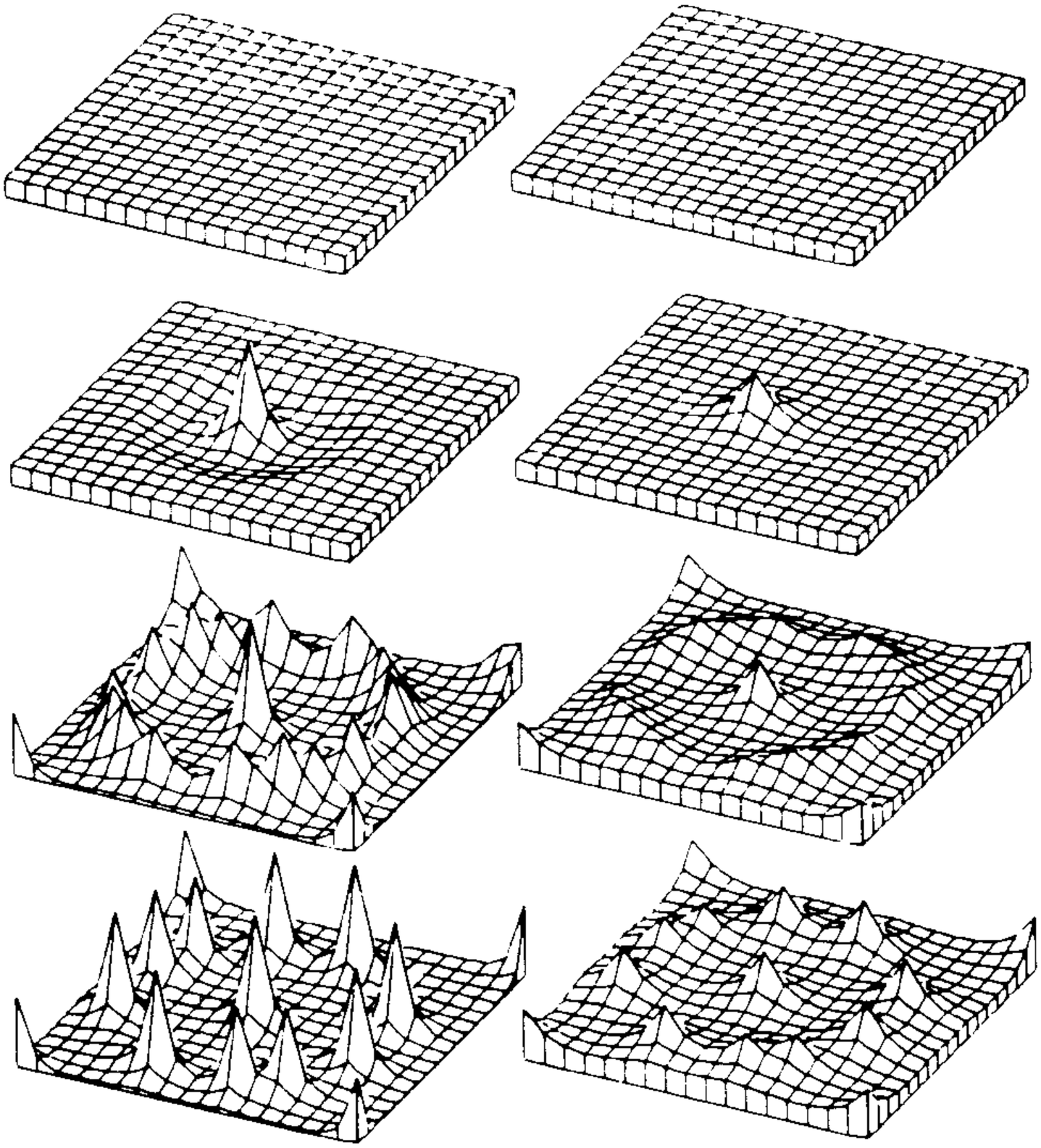

Fig. 10.3. Results of the morphogenetic model. Left column: activator concentration plottet over two dimensions. Right column: same for inhibitor. Rows refer to different times growing from above to below (computer solution). (After *H. Meinhardt, A. Gierer*: J. Cell Sci. **15**, 321 (1974))