

DEVELOPMENT OF RETINOTOPIC PROJECTIONS: AN ANALYTICAL TREATMENT

A. F. HÄUSSLER† and C. VON DER MALSBURG
Max-Planck-Institute for Biophysical Chemistry
Postfach 2841, D-3400 Göttingen, West Germany.

(Received April 22, 1982)

Abstract

The development of the synaptic connections between two neural fields (e.g. retina and tectum) from an undifferentiated initial state toward a topological projection is described by an appropriate system of differential equations. The equations are based simply on cooperative and competitive interactions between the individual synaptic contacts. In the case of one-dimensional fields it is shown that the system is able to select either of the two possible orientations and to produce a precise topological projection. This is done with the methods of synergetics: Linear analysis near the initial state, classification of the linear modes into principal and ancillary, adiabatic elimination of the latter from the original system and discussion of the resulting equations.

1. Introduction

A basic problem regarding brain organization is how ordered projections between different sheets of nerve cells are set up by fibres. A case which has been investigated experimentally and theoretically in detail is the projection between eye and brain. In the course of ontogenesis of vertebrate animals, each ganglion cell of the retina puts out a fibre which grows through the eye stalk to the brain. There it establishes synaptic contacts on cells of central structures such as the optic tectum (see Fig. 1). In some species these contacts on the tectum are initially rather random. In the adult animal, however, the retino-tectal connections are arranged retinotopically, i.e. neighbouring retinal cells project through their fibres onto neighbouring cells of the tectum. It follows that there must be some mechanism for rearranging the initially disordered contacts (for a review see Gaze (1978)).

A sorting mechanism which solves the problem has been presented in v.d. Malsburg and Willshaw (1977) and Willshaw and v.d. Malsburg (1979). The essence of that theory is the following: Suppose that each fibre has already grown from retina to tectum and has built many synaptic contacts on the tectum. A fibre moves over the tectum by strengthening its contacts in some parts of its ramification and by weakening them in others. These modifications obey the following rules.

Cooperativity.—The synaptic contacts on neighbouring tectal cells which are built by fibres of the same retinal region help each other to be strengthened.

Competition.—The contacts made by one fibre compete with each other. The same applies to the contacts on one tectal cell.

†A. F. Häussler died August 7, 1982, aged 35.

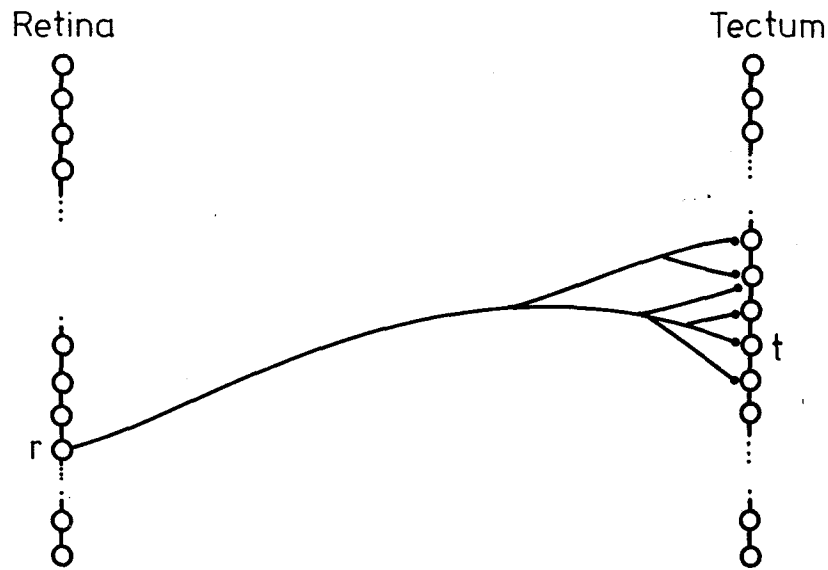


Fig. 1. Schematic illustration of a fibre with its synaptic contacts. Each retinal cell puts out a fibre which makes several synaptic contacts on cells of the tectum.

A fibre moves over the tectum by strengthening and weakening its contacts. These modifications are controlled by interactions between synaptic contacts.

In the simplified case of a retina and a tectum in the form of 'one-dimensional' chains of cells there is a convenient way to visualize these interactions in a matrix, with columns corresponding to retinal cells (or fibres) and rows corresponding to tectal cells (see Fig. 2). Each entry in the matrix is a weight characterizing the strength of connection between the corresponding retinal cell and tectal cell (the weight may stand for density and/or size of the synaptic contacts). Elevated weights which lie closely together in one region of the matrix increase by cooperativity. Due to competition, however, this growth must be compensated by the decrease of weights in the same column and in the same row (see Fig. 3). Hence an optimal growth-pattern is a diagonal, which corresponds to one of the two retinotopic mappings possible in the one-dimensional case. To install a specific orientation (e.g. nasal retina projecting to caudal tectum) the symmetry between orientations has to be broken by an additional mechanism. A convenient way is to assume that the initial configuration of weights slightly favours this orientation (see Fig. 4).

In Willshaw and v.d. Malsburg (1979) extensive computer simulations have shown that a system based on these ideas indeed establishes retinotopy as final configuration. The simulations did also account for the many types of experiments involving perturbations of the normal case. The details of the theory were adapted as closely as possible to known biological facts on the cellular level. In particular, a

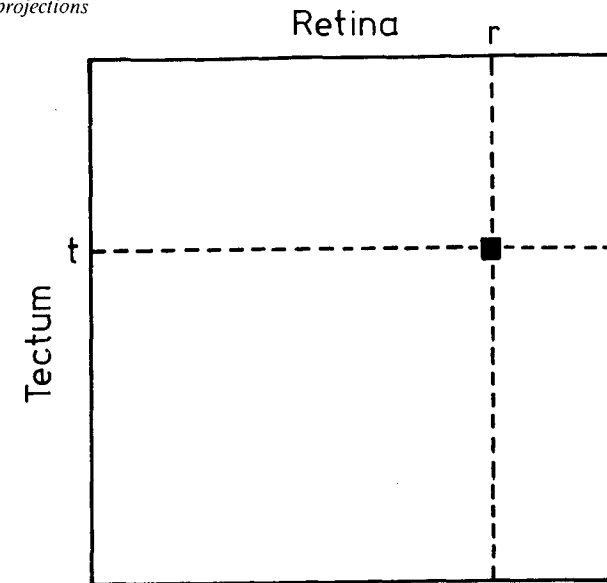


Fig. 2. Matrix display of connection-weights for 'one-dimensional' retina and tectum. The entry $w_{t,r}$ in column r and row t of the matrix is a weight characterizing the strength of connection between retinal cell (or fibre) r and tectal cell t (the weight may stand for density and/or size of the synaptic contacts). The area of the filled square is proportional to $w_{t,r}$.

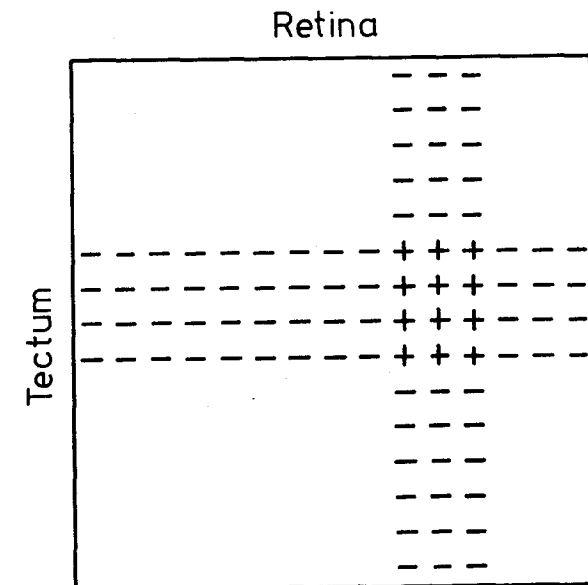


Fig. 3. Modification of weights. Elevated weights which lie closely together in the connection-matrix increase by cooperativity (+). Due to competition this growth is compensated by a decrease in the corresponding columns and rows (-).

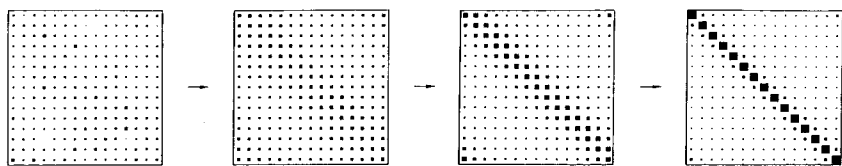


Fig. 4. Evolution according to modification rules. The figure shows an initial weight-configuration, two intermediate states and a final configuration as result of a numerical solution of the differential equations introduced in section 2.

Each diagonal of the connection-matrix corresponds to one of the two retinotopic projections which are possible in the case of 'one-dimensional' retina and tectum. The system evolves toward the retinotopic mapping of the orientation favoured in the initial state.

detailed system of chemical signals, called markers, was discussed. It explains how synaptic contacts lying near to each other on the tectum can sense the neighbourhood relationship of their retinal cells of origin. The differential equations based on these details have been discussed in v.d. Malsburg and Willshaw (1981).

The present study gives an analytical treatment of the theory. This is possible by considering a new set of differential equations. These incorporate the rules given above in a way which abstracts from the details of the cellular interactions, thereby putting more emphasis on the general features of the mechanism. In the case of one-dimensional chains it is shown that the system is able to select either of the two possible orientations and to develop into a precise topological projection. One may entertain the hope that a deeper understanding of the particular problem at hand will give insight into the way in which other specific neural connection systems are constructed during ontogenesis. Furthermore, it may also help to understand better how established neural networks in the adult organize structured activity patterns (see v.d. Malsburg (1981)).

The differential equations are introduced in sections 2 and 3. In section 4 we give an outline of the treatment, which is carried out in detail in the subsequent sections 5, 6 and 7, where we make use of the methods of synergetics (see Haken (1978)).

2. The analytical model

As the treatment of the two dimensional case, although possible, would be rather involved, let us assume that retina and tectum both are one-dimensional chains. We assume furthermore that these chains contain the same number N of cells. Let us introduce the real number $w_{t,r}$ as a weight characterizing the strength of the connection $\langle t,r \rangle$ between the retinal cell (or fibre) r and the tectal cell t , possibly established by several synaptic contacts. The weights define a real function \mathbf{w} on the domain $\{\langle t,r \rangle | 0 \leq t,r < N\}$, which can be displayed in an $N \times N$ -array, the connection-matrix (see Fig. 2). These configurations form a linear space \mathcal{W} of the finite dimension N^2 .

Differential equations for the modification of weights.—This system for the rate of change of the weights $w_{t,r}$, $0 \leq t,r < N$, was developed along the guiding lines discussed above and is given as follows:

$$(2.1) \quad \dot{w}_{t,r} = f_{t,r}(\mathbf{w}) - \frac{1}{2} w_{t,r} \left(\frac{1}{N} \sum_{t'} f_{t',r}(\mathbf{w}) + \frac{1}{N} \sum_{r'} f_{t,r'}(\mathbf{w}) \right),$$

with

$$(2.2) \quad f_{t,r}(\mathbf{w}) = \alpha + \beta w_{t,r} \cdot C_{t,r}(\mathbf{w}),$$

$$(2.3) \quad C_{t,r}(\mathbf{w}) = \sum_{t',r'} c(t,t',r,r') w_{t',r'}.$$

This is a first-order system of cubic equations in N^2 variables. The growth-rate of the weight $w_{t,r}$ is $f_{t,r}(\mathbf{w})$. It consists of a positive constant α which represents the formation-rate of synapses on the tectum by incoming retinal fibres, and a rate for cooperativity which is constituted by the cooperativity-coefficient $C_{t,r}(\mathbf{w})$ with a positive factor β . The cooperativity-coefficient decomposes into contributions of the form $c(t,t',r,r') w_{t',r'}$. Each contribution stands for cooperative help of the synaptic contacts made by retinal fibre r' on tectal cell t' to the synaptic contacts between retinal fibre r and tectal cell t . The coefficient $c(t,t',r,r')$ depends on the cell-distance $|t-t'|$ between the location of the synapses on the tectum as well as the cell-distance $|r-r'|$ between the retinal cells of origin of their fibres. The closer $\langle t,r \rangle$ and $\langle t',r' \rangle$ are to each other in both indices the larger is this coefficient (see Fig. 5). Biological considerations suggest that it is reasonable to assume that $c(t,t',r,r')$ can be decomposed into a product $c_T(|t-t'|) \cdot c_R(|r-r'|)$. Note that we refer only to distance, not to position or orientation. In section 5 we will see that, according to these assumptions, $C_{t,r}(\mathbf{w})$ is simply a smoothed version of \mathbf{w} . The negative term in (2.1) limits the weights during evolution and will be discussed in section 3.

Periodicity assumption.—Unfortunately these assumptions about the coefficients are too general for an analytical treatment because boundaries lead to complications. We avoid these difficulties by assuming, for retina and for tectum, that the endpoints of the neural chains are neighbours. Thus retina and tectum are both considered as cyclic chains with N cells (for convenience, we will consider from now on the indices t,r as integers modulo N , i.e. $t,r \in \mathbb{Z}_N$). All this together leads to a specification of (2.3) as follows:

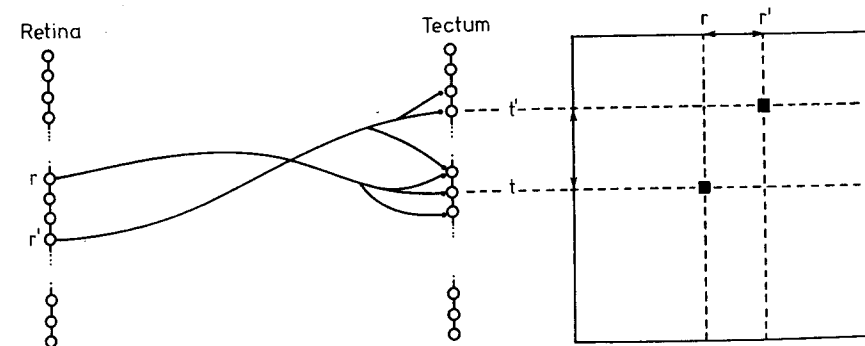


Fig. 5. Cooperativity.

$$(2.4) \quad C_{t,r}(\mathbf{w}) = \sum_{t',r'} c(t-t', r-r') w_{t',r'}$$

with $c(t-t', r-r') = c_T(t-t') \cdot c_R(r-r')$. The factors are real coefficients, having the following properties:

$$(2.5) \quad 0 \leq c_T(m), 0 \leq c_R(n), m, n \in Z_N;$$

$$(2.6) \quad c_T(m) = c_T(-m), c_R(n) = c_R(-n), m, n \in Z_N;$$

$$(2.7) \quad c_T(m) > c_T(m') \text{ for all } m, m' \text{ with } 0 \leq m < m' \leq \frac{N}{2};$$

$$(2.8) \quad c_R(n) > c_R(n') \text{ for all } n, n' \text{ with } 0 \leq n < n' \leq \frac{N}{2}.$$

The positive factor β in (2.2) allows us to put

$$(2.9) \quad \sum_m c_T(m) = \sum_n c_R(n) = 1.$$

3. Competition

The choice of the limitation-term, i.e. the negative term in (2.1), has been guided by the assumption that the total weight of all contacts made by one retinal fibre, as well as the total weight of all contacts on one tectal cell should be kept near to certain saturation values. A momentary overshoot is compensated by the un-specific weakening of all the synaptic contacts involved. As we will see, this leads to sum-rules, bounds, stationary solutions, competition and selection.

Saturation value.—If we had instead of (2.1) the equation

$$\dot{w}_{t,r} = f_{t,r}(\mathbf{w}) - w_{t,r} \frac{1}{N} \sum_{t'} f_{t',r}(\mathbf{w}),$$

then we would obtain for $W_r^R = \sum_{t'} w_{t',r}$ (i.e. the sum over all weights within the column r)

$$\dot{W}_r^R = -\frac{1}{N} \left(\sum_{t'} f_{t',r}(\mathbf{w}) \right) (W_r^R - N).$$

This shows that in any evolution (within the bounds introduced in the next paragraph) the sum W_r^R would converge toward the saturation value N ; hence a sum-rule for the connection-weights of any particular retinal fibre would be established. The actual term in (2.1) is the mean of two terms. The additional term by itself would establish a sum-rule for all connection-weights with each tectal cell. As in the complete form both rules interfere there is no direct interpretation in terms of a sum-rule.

Upper and lower bounds for the connection-weights.—If all weights $w_{t,r}$ satisfy $0 \leq w_{t,r} \leq N$ in an initial configuration, then the evolution of the system remains within these two bounds. This can be shown as follows: The assumption $0 \leq w_{t,r} \leq N$ for all $t, r \in Z_N$ yields the inequality $0 \leq C_{t,r} \leq N$ for all $t, r \in Z_N$. A lower bound for the rate of change of any particular $w_{t,r}$ is thus given by $\alpha - w_{t,r}$ ($\alpha + \beta N^2$). Hence a small $w_{t,r}$ is prevented by the positive rate α from becoming

zero. On the other hand, an upper bound for the rate of change is given by $-(N-1)\alpha + (\alpha + \beta N)(N - w_{t,r})$. For a weight slightly below N , the rate is dominated by $-(N-1)\alpha$ and is thus prevented from exceeding the upper bound.

All further investigations will concentrate on solutions within these two bounds. For such configurations \mathbf{w} all the coefficients $C_{t,r}(\mathbf{w})$ and $f_{t,r}(\mathbf{w})$ are positive.

Stationary homogeneous solution.—The system has the stationary homogeneous solution $w_{t,r} = 1, t, r \in Z_N$, which we will designate by 1. This solution is independent of α and β ; its value is fixed by the choice of the two coefficients $1/N$ in the limitation-term. There are two further st.h. solutions, which are, however, imaginary, as α and β are considered to be positive.

Competition and selection (see Fig. 6).—The growth-rate $f_{t,r}(\mathbf{w})$ consists of the two independent contributions α and $\beta w_{t,r} \cdot C_{t,r}(\mathbf{w})$. Both are affected separately by the limitation-term, which we see after collecting the parts of (2.1) containing α on the one and β on the other hand:

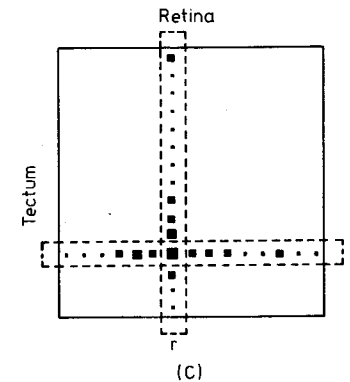
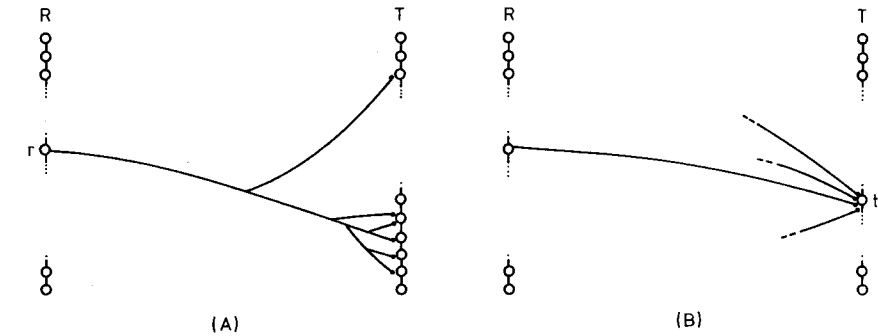


Fig. 6. Illustration of types of competition: (A) between the synaptic contacts built by a retinal fibre r , (B) between the synaptic contacts on a tectal cell t . (C) All weights competing with $w_{t,r}$ in connection-matrix arrangement.

$$(3.1) \quad \dot{w}_{t,r} = \alpha(1 - w_{t,r}) + \beta w_{t,r} \left(C_{t,r}(\mathbf{w}) - \frac{1}{2} \left(\frac{1}{N} \sum_{t'} w_{t',r} \cdot C_{t',r}(\mathbf{w}) + \frac{1}{N} \sum_{r'} w_{t,r} \cdot C_{t,r}(\mathbf{w}) \right) \right).$$

The effect of these two parts on the behaviour of the system is totally dissimilar and will be discussed now. As the dependence of $C_{t,r}$ on \mathbf{w} will not be important here, let us assume for the moment fixed values for $C_{t,r}$ and drop the \mathbf{w} in the notation.

$\alpha \gg \beta$: In this case any evolution within the bounds $\mathbf{0}$ and \mathbf{N} will end up in the neighbourhood of $\mathbf{1}$.

$\beta \gg \alpha$: The $C_{t,r}$ acts as a rate-coefficient for $w_{t,r}$. Whether $w_{t,r}$ grows or diminishes depends on the comparison of $C_{t,r}$ with the value of the negative term in the β -part of (3.1). In this term all connection-weights of the retinal fibre r and all those of the tectal cell t are involved. This gives rise to a complicated coupling between all equations of the system. As in the previous consideration, let us again restrict ourselves to one term. This would lead to the following β -part

$$\beta w_{t,r} \left(C_{t,r} - \frac{1}{N} \sum_{t'} w_{t',r} \cdot C_{t',r} \right).$$

The value of the negative term would be the mean of all $w_{t',r} \cdot C_{t',r}$, $t' \in Z_N$, which would depend on all the weights and cooperativity-coefficients for the particular connections of the retinal fibre r only. For all $w_{t',r}$, $t' \in Z_N$, the values would be the same and act as a common threshold: If $C_{t',r}$ were larger than this threshold, then $w_{t',r}$ would grow, otherwise it would diminish. Starting with small weights, this threshold would be shifted to higher values during evolution (in the threshold the large coefficients are multiplied with their corresponding fast growing weights). Fewer and fewer weights would continue to grow. Finally only the weight with the highest cooperativity-coefficient would still grow, for $\alpha=0$ up to the value N . In this process the sum over all $w_{t',r}$, $t' \in Z_N$, tends to the value N . In other words: All connections $\langle t', r \rangle$, $t' \in Z_N$, of the retinal fibre r would compete and the one with the highest cooperativity-coefficient would be selected, so that eventually the retinal fibre r would be connected with just one tectal cell (competition in columns). The similar term for rows would lead to competition and selection among connections $\langle t, r'' \rangle$, $r'' \in Z_N$, of the same tectal cell t (competition in rows). [The same type of differential equation is well-known from population selection theory. There the growth-rates of different species are controlled by individual rate-coefficients and the total population is limited. The species with the highest rate-coefficient survives, all others die out.]

The actual term is again the mean of both terms. For a particular connection both influences interfere with each other. A consequence for the selection behaviour is illustrated by the fact that for $\alpha=0$ the typical stationary solutions can be described as configurations which have one weight equal to N in each column and each row and all other weights equal to 0. These correspond to one-to-one projections of the retina onto the tectum. Most of these solutions are unstable, depending on the coefficients $C_{t,r}$, $t, r \in Z_N$.

Conclusion.—The β -part can give rise to extreme final configurations, such as one-to-one mappings of retina onto tectum, whereas the α -part has the tendency to level out differences between the weights. The course of events, however, will depend not only on the choice of α and β , but also on the initial configuration and on the form of the function $C_{t,r}(\mathbf{w})$.

4. Outline of the treatment

An explicit integration or even an overview over all the stationary solutions of this system of N^2 variables is hardly possible. However, at least the evolution from certain initial configurations toward a retinotopic final configuration can be successfully investigated with the methods of synergetics. Before entering into details we will, in this section, give a rough sketch of the treatment.

Change of time scale.—A multiplicative factor on the right hand side of (2.1) or (3.1) corresponds to a change of time scale, thus let us assume $\beta=1$ from now on.

Initial configuration.—Let us assume that each retinal fibre has made synaptic contacts all over the tectum and consider as initial state a configuration $\mathbf{w}(0)$ which is close to the st.h. solution $\mathbf{1}$.

Linear analysis.—Since $\mathbf{w}(0)$ is assumed to be close to the st.h. solution $\mathbf{1}$, we introduce the deviation from $\mathbf{1}$ as appropriate new variable. The system of differential equations for the deviation can be given explicitly and consists of a linear, a quadratic and a cubic term. As long as we consider the evolution within a small neighbourhood of $\mathbf{1}$, it is sufficient to approximate the system by the linear term. As in all linear systems, there are certain deviation-patterns — eigenfunctions of the linear system — which preserve their shapes and increase or decrease independently in amplitude depending on the sign of their eigenvalue. In the present case all these patterns and their eigenvalues can be calculated explicitly and the decomposition of the initial configuration $\mathbf{w}(0)$ with respect to these independently evolving deviation-patterns would lead to the solution of the linearly approximated system. It turns out that the spectrum of eigenvalues is real and lies within the interval $[-\alpha-1, -\alpha+1]$. The relative position of the values is determined by the coefficients $c(m,n)$, $m,n \in Z_N$, occurring in the β -part, whereas the rate α determines the position of the spectrum as a whole. Thus α is a control parameter for the system's behaviour in the neighbourhood of $\mathbf{1}$. The most interesting patterns are those which correspond to the maximal eigenvalue, because they are amplified as long as there are positive eigenvalues at all. There are several deviation-patterns associated with the maximal eigenvalue. Two of the patterns have the form of a cosine with positive values along one of the diagonals of the connection-matrix and negative values elsewhere. This multiplicity is due to the intrinsic symmetry of the problem, no orientation in retina and tectum. The others correspond to diagonals in shifted positions and are due to the periodicity assumption. All these patterns have the highest eigenvalue because they are strongly amplified by cooperativity (this is the point where the neighbourhood relationships in retina and tectum enter the discussion) and not affected by limitation as they preserve sums in columns and

rows. Growth of one of these patterns expresses the tendency to establish a retinotopic projection. The patterns which correspond to smaller eigenvalues do not have this quality. Thus let the parameter α be just large enough for all these undesired patterns to be damped.

Higher-order analysis.—The linear term selectively amplifies the diagonal-pattern components of the initial configuration $\mathbf{w}(0)$, but it cannot discriminate between the two diagonal directions. In contrast, the full set of differential equations describes interactions between patterns by which in particular the two diagonal-patterns compete with each other. The one which is favoured in the initial configuration has a selective advantage and overcomes the other, which has to decay. This will be shown by an adiabatic elimination of the damped patterns, which leads to a system of differential equations in the amplitudes of the diagonal-patterns alone.

The final configuration.—The winning diagonal-pattern component develops into a narrow retinotopic projection by activating precisely those of the damped patterns which can contribute to its narrowing. By a gradual decrease of the parameter α to zero a one-to-one retinotopic projection can be obtained.

Development of a retinotopic projection.—The parameter α represents the formation-rate of synaptic contacts on the tectum by incoming retinal fibres. It is used as control parameter. Initially, α is kept near to the critical value, until one of the diagonal-patterns is selected. Then α is lowered close to zero, letting the system settle into a retinotopic state.

5. Linear analysis

To simplify notation, we introduce in W , the linear space of all configurations, the multiplication $\mathbf{x} \cdot \mathbf{y}$ and the linear operators C , B and P : For $t, r \in Z_N$, let be

$$(5.1) \quad (\mathbf{x} \cdot \mathbf{y})_{t,r} = x_{t,r} y_{t,r},$$

$$(5.2) \quad C_{t,r}(\mathbf{x}) = \sum_{t',r'} c(t-t', r-r') x_{t',r'} \text{ (identical with 2.4),}$$

$$(5.3) \quad B_{t,r}(\mathbf{x}) = \frac{1}{2} \left(\frac{1}{N} \sum_{t'} x_{t',r} + \frac{1}{N} \sum_{r'} x_{t,r'} \right),$$

$$(5.4) \quad P_{t,r}(\mathbf{x}) = \frac{1}{N^2} \sum_{t',r'} x_{t',r'}.$$

The coefficients $c(m,n)$, $m,n \in Z_N$, have been introduced in Section 2 and have several properties of which full use is made in this section. In particular the dependence of $C_{t,r}$ on \mathbf{w} , which we have so far left out of consideration, will become clear. Note that $C(\mathbf{1}) = B(\mathbf{1}) = P(\mathbf{1}) = \mathbf{1}$.

The system (2.1) of differential equations for the modification of the weights can now be written in concise form

$$(5.5) \quad \dot{\mathbf{w}} = \alpha \mathbf{1} + \beta \mathbf{w} \cdot C(\mathbf{w}) - \mathbf{w} \cdot B(\alpha \mathbf{1} + \beta \mathbf{w} \cdot C(\mathbf{w})),$$

or, an analogy to (3.1), divided into an α -part and a β -part:

$$(5.6) \quad \dot{\mathbf{w}} = -\alpha(\mathbf{w} - \mathbf{1}) + \beta \mathbf{w} \cdot (C(\mathbf{w}) - B(\mathbf{w} \cdot C(\mathbf{w}))).$$

Let us introduce the deviation $\mathbf{v} = \mathbf{w} - \mathbf{1}$, for which the full system reads (with $\beta = 1$):

$$(5.7) \quad \dot{\mathbf{v}} = L(\mathbf{v}) + Q(\mathbf{v}) + K(\mathbf{v})$$

with

$$(5.8) \quad L(\mathbf{v}) = -\alpha \mathbf{v} + C(\mathbf{v}) - B(\mathbf{v}) - B(C(\mathbf{v})), \text{ the linear term,}$$

$$(5.9) \quad Q(\mathbf{v}) = \mathbf{v} \cdot (C(\mathbf{v}) - B(\mathbf{v}) - B(C(\mathbf{v}))) - B(\mathbf{v} \cdot C(\mathbf{v})), \text{ the quadratic term,}$$

$$(5.10) \quad K(\mathbf{v}) = -\mathbf{v} \cdot B(\mathbf{v} \cdot C(\mathbf{v})), \text{ the cubic term.}$$

The α -part contributes to the linear term only. All other contributions are due to the β -part.

Eigenfunctions and eigenvalues.—The main reason for the linear term (5.8) to have explicit eigenfunctions is its symmetry property. Due to the periodicity assumption, the abelian group $C_N \times C_N$ acts in a natural way on the function space W of configurations (C_N is the cyclic group of order N). All operators which appear in (5.8) are symmetric under these transformations representing the group in W . Thus the operators decompose with respect to the invariant subspaces of W associated with the different irreducible subrepresentations of $C_N \times C_N$. Since the representation in W is regular and the group abelian, these subspaces are one-dimensional and therefore eigenspaces of the operators. The computation of the subspaces can be done in a straightforward way with the help of the known characters of the different irreducible representations of $C_N \times C_N$. It leads to a system of N^2 complex-valued eigenfunctions for the linear operators C , B and P : For any pair $\langle k, l \rangle$, $k, l \in Z_N$, there is an eigenfunction $e^{k,l}$ with

$$(5.11) \quad e_{t,r}^{k,l} = \exp(i \frac{2\pi}{N} (kt + lr)), \quad t, r \in Z_N.$$

These N^2 complex functions are linearly independent and form a basis for the complexification W^C of W . For $k=l=0$ we have the constant function $\mathbf{1}$, the others are periodic complex harmonics in the connection-matrix. The lack of higher frequencies is due to the fact that we deal with discrete chains for retina and tectum.

This way of obtaining eigenfunctions by symmetry arguments is rather abstract, but it demonstrates the power of symmetry assumptions for explicit calculations in high-dimensional problems. The result of this reasoning can be confirmed directly by letting the operators act on these functions. In addition, we thereby obtain expressions for the eigenvalues:

$$(5.12) \quad \begin{aligned} C(e^{k,l}) &= \gamma^{k,l} e^{k,l} \\ &= \sum_{t',r'} c(-t', -r') \exp(i \frac{2\pi}{N} (kt' + lr')) e^{k,l}, \end{aligned}$$

$$(5.13) \quad B(e^{k,l}) = \begin{cases} 1 & , \text{ for } k=l=0, \\ \frac{1}{2}e^{k,l} & , \text{ for } k=0, l \neq 0 \text{ or } k \neq 0, l=0, \\ 0 & , \text{ otherwise;} \end{cases}$$

$$(5.14) \quad P(e^{k,l}) = \begin{cases} 1 & , \text{ for } k=l=0, \\ 0 & , \text{ otherwise.} \end{cases}$$

Note that in distinction to the eigenfunctions the eigenvalues depend on the coefficients $c(m,n)$, $m,n \in Z_N$. By (2.5) and (2.9) we have $c(m,n) \in \mathbf{R}^+$ and $\sum_{m,n} c(m,n) = 1$, thus each eigenvalue $\gamma^{k,l}$, $k,l \in Z_N$, is a convex sum of the complex vectors $\{\exp(i 2\pi/N \cdot (kt' + lr')) | t', r' \in Z_N\}$. These vectors lie on the circle $\{z | |z|=1\}$, so that the inequality

$$(5.15) \quad |\gamma^{k,l}| \leq 1$$

holds for all $k,l \in Z_N$. Especially $\gamma^{0,0} = 1$, which restates the fact that $C(\mathbf{1}) = \mathbf{1}$.

The spectrum $\{\lambda^{k,l} | k,l \in Z_N\}$ of the linearized system (5.8) is obtained by applying $L(\mathbf{v})$ to these eigenfunctions:

$$(5.16) \quad \lambda^{k,l} = \begin{cases} -\alpha - 1 & , \text{ for } k=l=0, \\ -\alpha + \frac{1}{2}(\gamma^{k,l} - 1), & \text{ for } k=0, l \neq 0 \text{ or } k \neq 0, l=0, \\ -\alpha + \gamma^{k,l} & , \text{ otherwise.} \end{cases}$$

These results on eigenfunctions and eigenvalues bear a resemblance to those given in Turing (1952), where reaction-diffusion systems of morphogens in a ring of cells are investigated.

By an appropriate choice of the parameter α the highest of these eigenvalues can be selected as the only positive one. The aim of the following discussion is to show that the highest eigenvalue of the spectrum corresponds to the desired diagonal-patterns.

Real modes.—The eigenvalues $\gamma^{k,l}$ of C are real and satisfy

$$(5.17) \quad \gamma^{k,l} = \gamma^{\pm k, \pm l}$$

for all $k,l \in Z_N$. This is due to $c(m,n) \in \mathbf{R}$ and the symmetry property $c(m,n) = c_T(m) \cdot c_R(n) = c(\pm m, \pm n)$ which follows from (2.5) and (2.6). Hence the spectrum (5.16) of the linear term is enclosed within the interval $[-\alpha - 1, -\alpha + 1]$ of the real axis and we have for $k,l \in Z_N$

$$(5.18) \quad \lambda^{k,l} = \lambda^{\pm k, \pm l}.$$

This equality allows us to introduce a system of real eigenfunctions by the combination of complex conjugate eigenfunctions $e^{k,l}$ and $e^{-k,-l}$:

$$(5.19) \quad \begin{aligned} c^{k,l} &= \frac{1}{2}(e^{k,l} + e^{-k,-l}), & c_{t',l}^{k,l} &= \cos\left(\frac{2\pi}{N}(kt + lr)\right), \\ s^{k,l} &= -\frac{i}{2}(e^{k,l} - e^{-k,-l}), & s_{t',l}^{k,l} &= \sin\left(\frac{2\pi}{N}(kt + lr)\right). \end{aligned}$$

These $2N^2$ functions $\{c^{k,l}, s^{k,l} | k,l \in Z_N\}$ are all eigenfunctions (or modes) of the operators that we consider. Obviously, they are not independent, since $c^{k,l} = c^{-k,-l}$, $s^{k,l} = -s^{-k,-l}$, $s^{0,0} = 0$, and, as the indices are modulo N , $s^{0,N/2} = s^{N/2,0} = s^{N/2,N/2} = 0$ for even N . A reduction to an independent system, however, would be straightforward.

For any $k,l \in Z_N$ the two modes $c^{k,l}$ and $s^{k,l}$ generate a real subspace of W . If $a = \rho \cos \psi$, $b = \rho \sin \psi$ for $\rho \geq 0$ and $\psi \in (-\pi, \pi]$, then $(ac^{k,l} + bs^{k,l})_{l,r} = \rho \cos(2\pi/N(kt + lr) - \psi)$; thus such a subspace consists of all functions obtained from $\rho c^{k,l}$ by phase-shifts. These subspaces are two dimensional except in those

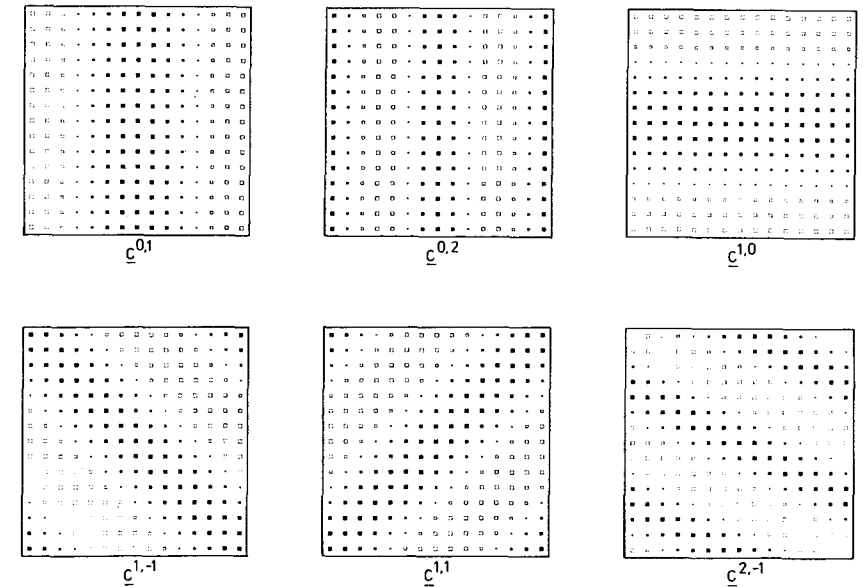


Fig. 7. Some of the modes. They are periodic harmonics in the matrix. $c^{0,1}$ and $c^{0,2}$ are called column-modes, $c^{1,0}$ is a row-mode, the remaining three are oblique modes. $c^{1,1}$ and $c^{1,-1}$ are the two diagonal-modes. In these illustrations the centre of the matrix has indices $t=r=0$. White squares stand for negative values.

The linear approximation of the differential equation (5.7) for the deviation $\mathbf{v} = \mathbf{w} - \mathbf{1}$ ($\mathbf{1}$ is the homogeneous stationary solution of the system) leads to N^2 modes, independently amplified or damped deviation-patterns. If the rate α (a parameter characterizing the formation-rate of synaptic contacts on the tectum by incoming retinal fibres) is larger than γ (a value characterizing cooperativity), then all the modes are damped. If α is slightly smaller than γ , i.e. $\lambda = -\alpha + \gamma > 0$, then the diagonal-modes are the only non-damped ones; they are amplified by cooperativity and not affected by competition. Therefore we consider α as control parameter of the system.

cases with $\mathbf{s}^{k,l} = \mathbf{0}$, in which case they are one-dimensional. We refer to a mode with $k=0, l \neq 0$ or $k \neq 0, l=0$ as a column-mode or row-mode, respectively. The mode $\mathbf{1}$ is called constant-mode. All other modes are called oblique modes. In Figure 7 some real modes are illustrated.

Diagonal-modes.—We refer to the modes $\mathbf{c}^{1,1}$ and $\mathbf{c}^{1,-1}$ as diagonal-modes, and to all the functions obtained from these by phase-shift as ‘broken diagonals’. These functions generate a subspace of W of dimension four. Any function of this subspace is a superposition of two (broken) diagonals with different orientation. The space is furthermore an eigenspace of the operator C as well as of the linear term L of the system, with eigenvalues $\gamma^{\pm 1, \pm 1}$ and $\lambda^{\pm 1, \pm 1}$ respectively.

Maximal eigenvalue of the spectrum.—First note that the α -part provides a negative contribution to all eigenvalues of the spectrum (5.16). The remaining contribution originates from the β -part of the system. The constant-mode, the column-modes and row-modes are affected by limitation in such a way that their eigenvalues (for any choice of $\alpha > 0$) are negative because of (5.15), whereas the oblique modes are not affected at all. This shows that limitation tends to keep sums within columns and rows constant equal to the saturation value N . We are left now with the oblique modes and have to look for those with the maximal eigenvalue $\lambda^{k,l}$, i.e. according to (5.16) the maximal $\gamma^{k,l}$.

Eigenvalues of the operator C .—The coefficients $c(m,n)$, $m,n \in Z_N$, of C can be regarded as an element \mathbf{c} of the function space W . The expansion of \mathbf{c} in the system of eigenfunctions is

$$(5.20) \quad \mathbf{c} = \frac{1}{N^2} \sum_{k,l} \gamma^{k,l} \mathbf{e}^{k,l} = \frac{1}{N^2} \sum_{k,l} \gamma^{k,l} \mathbf{e}^{k,l},$$

a relation which gives some insights into the connection between the coefficients \mathbf{c} and the eigenvalues of C .

Proof of (5.20).—Let \mathbf{d} be the function in W with $d_{0,0} = 1$ and 0 otherwise. We have $\mathbf{d} = N^{-2} \sum_{k,l} \mathbf{e}^{k,l}$. By application of C on both sides we obtain \mathbf{c} on the left hand side by (5.2) and $N^{-2} \sum_{k,l} \gamma^{k,l} \mathbf{e}^{k,l}$ on the right hand side, since the $\mathbf{e}^{k,l}$ are eigenfunctions of C with $\gamma^{k,l}$ as eigenvalues. The second expansion follows from (5.17) and (5.19).

From (2.7) and (2.8) it follows that \mathbf{c} is ‘bell-shaped’ and maximal in $m=n=0$, a fact of which we have made no use until now. Such a shape suggests that the low-frequency contributions dominate in the expansion (5.20) of \mathbf{c} , which implies that among the oblique mode components the diagonal ones are the largest. To make this argument precise, let us consider the expansions of c_T and c_R in harmonics (k and l are indices):

$$(5.21) \quad c_T(m) = \frac{1}{N} \sum_k \gamma_T^k \exp(i \frac{2\pi}{N} km), \quad m \in Z_N,$$

$$(5.22) \quad c_R(n) = \frac{1}{N} \sum_l \gamma_R^l \exp(i \frac{2\pi}{N} ln), \quad n \in Z_N.$$

With (2.5), (2.6) and (2.9) we obtain $\gamma_T^k, \gamma_R^l \in \mathbf{R}$, $\gamma_T^k = \gamma_T^{-k}$, $\gamma_R^l = \gamma_R^{-l}$ for all $k, l \in Z_N$, and $\gamma_T^0 = \gamma_R^0 = 1$.

By comparing (5.20) with the product of (5.21) and (5.22), we obtain

$$(5.23) \quad \gamma^{k,l} = \gamma_T^k \gamma_R^l, \quad k, l \in Z_N,$$

and furthermore

$$(5.24) \quad \gamma^{k,l} = \gamma^{k,0} \gamma^{0,l}, \quad k, l \in Z_N.$$

Now, the properties (2.7), (2.8) imply that in the expansions (5.21), (5.22) the amplitude of the first harmonic is positive and larger than that of all higher ones, which can be proved with the help of the Identity of Abel (a discrete version of partial integration). Thus, we have

$$(5.25) \quad \begin{aligned} \gamma_T^k &= \gamma_T^{-1} > |\gamma_T^k|, \quad 1 < k < N-1, \\ \gamma_R^l &= \gamma_R^{-1} > |\gamma_R^l|, \quad 1 < l < N-1. \end{aligned}$$

By (5.23) and (5.25), it is now obvious that among the oblique modes the (broken) diagonal-modes have the largest eigenvalue, which is $\gamma^{\pm 1, \pm 1}$.

Conclusion.—The largest value of the spectrum (5.16) of the linear term is the eigenvalue of the (broken) diagonal-modes, i.e. $\lambda^{\pm 1, \pm 1} = -\alpha + \gamma^{\pm 1, \pm 1}$. Let us designate $\lambda^{\pm 1, \pm 1}$ and $\gamma^{\pm 1, \pm 1}$ as λ and γ , respectively. According to the linear analysis an appropriate choice for α is such that

$$(5.26) \quad \lambda = -\alpha + \gamma > 0 > \lambda_a$$

where λ_a designates the maximal eigenvalue of the remaining modes. This choice secures that for any initial configuration in the neighbourhood of $\mathbf{1}$ the (broken) diagonal-mode components grow, whereas all other components are damped.

6. Higher order analysis

The particular choice we made in the last section for the control parameter α leads to a decomposition of $\mathbf{v} = \mathbf{w} - \mathbf{1}$ into a principal component \mathbf{v}_p which is the superposition of (broken) diagonal-modes, and an ancillary component \mathbf{v}_a lying in the subspace generated by all remaining modes. According to the linear approximation, \mathbf{v}_p will grow with the slightly positive rate-coefficient $\lambda = -\alpha + \gamma$, whereas \mathbf{v}_a will decay to zero with a damping coefficient of at least λ_a . Obviously, the linear approximation is not sufficient to describe the system’s evolution toward a retinotopic projection. Our analysis has to include the non-linear terms by which the different diagonal-mode components as well as the two components \mathbf{v}_p and \mathbf{v}_a interact. Nevertheless, since the linear term closely approximates the system in the neighbourhood of $\mathbf{1}$, we keep the distinction between \mathbf{v}_p and \mathbf{v}_a . The system (5.7) can be decomposed into contributions to changes of the components \mathbf{v}_p and \mathbf{v}_a :

$$(6.1) \quad \dot{\mathbf{v}}_p = L(\mathbf{v}_p) + Q_p(\mathbf{v}_p + \mathbf{v}_a) + K_p(\mathbf{v}_p + \mathbf{v}_a),$$

$$(6.2) \quad \dot{\mathbf{v}}_a = L(\mathbf{v}_a) + Q_a(\mathbf{v}_p + \mathbf{v}_a) + K_a(\mathbf{v}_p + \mathbf{v}_a).$$

Here we have used

$$(6.3) \quad L_p(\mathbf{v}_p + \mathbf{v}_a) = L(\mathbf{v}_p), \quad L_a(\mathbf{v}_p + \mathbf{v}_a) = L(\mathbf{v}_a).$$

Amplitudes of modes as new variables.—Let us consider the decomposition

$$(6.4) \quad \mathbf{v} = \sum_{k,l} \zeta_{k,l} \mathbf{e}^{k,l}$$

into the modes $\mathbf{e}^{k,l}$ with time-dependent amplitudes $\zeta_{k,l}$. The choice of the complex modes allows us to use the convenient product property

$$(6.5) \quad \mathbf{e}^{k,l} \cdot \mathbf{e}^{k',l'} = \mathbf{e}^{k+k',l+l'}.$$

The real deviations \mathbf{v} are characterized by

$$(6.6) \quad \zeta_{k,l} = \bar{\zeta}_{-k,-l}, \quad k,l \in Z_N.$$

The inversion formula of (6.4) is

$$(6.7) \quad \zeta_{k,l} = \frac{1}{N^2} \sum_{t,r} v_{t,r} \exp(-i \frac{2\pi}{N} (kt + lr)), \quad k,l \in Z_N.$$

This equation follows directly from $\zeta_{k,l} \mathbf{1} = P(\mathbf{v} \cdot \mathbf{e}^{-k,-l})$, which holds by (6.4), (6.5) and (5.14).

The aim of this section.—We want to study the system given now by (6.1) and (6.2). Insertion of (6.4) leads to a system of differential equations for the N^2 amplitudes $\zeta_{k,l}$, $k,l \in Z_N$. This, however, is as complicated as the original system. We therefore will reduce the system radically by the elimination of the ancillary modes, making use of the fact that these modes are all damped by the linear term. We then will be left with approximate differential equations in the four degrees of freedom of the principal component

$$(6.8) \quad \mathbf{v}_p = \zeta_{1,1} \mathbf{e}^{1,1} + \zeta_{-1,-1} \mathbf{e}^{-1,-1} + \zeta_{1,-1} \mathbf{e}^{1,-1} + \zeta_{-1,1} \mathbf{e}^{-1,1}.$$

We shall find the interactions between these different principal modes to be competitive, eventually leading to the selection of the mode that was favoured in the initial configuration.

It is advantageous to proceed with the approximation in two steps. In the first step, (6.1) is simplified by putting \mathbf{v}_a equal to zero. This leads to the intermediate system (6.15), which will turn out to already have the correct qualitative structure. However, the assumption $\mathbf{v}_a = \mathbf{0}$ is too radical, since in reality the ancillary modes, although damped, are excited to a finite magnitude by the principal modes through the quadratic and cubic terms in (6.2). In the second step, therefore, \mathbf{v}_a is eliminated by adiabatically approximating (6.2), giving \mathbf{v}_a as a function of \mathbf{v}_p , which then is inserted into (6.1). The resulting equation finally is approximated to third-order. In all these considerations transient effects are entirely neglected. This method of deriving differential equations for amplitudes of principal modes by adiabatic

elimination of the ancillary modes has been elaborated in Haken (1975a, 1975b, 1978).

Bounds for the amplitudes.—According to our discussion in section 3 and our assumption on the initial configuration, \mathbf{w} is real and positive at all times. We therefore have the inequality

$$(6.9) \quad |\zeta_{k,l}| \leq 1 + \zeta_{0,0} \quad k,l \in Z_N, \quad \langle k,l \rangle \neq \langle 0,0 \rangle.$$

This is a minimal test for the validity of any approximate result. Proof of (6.9): Since $\mathbf{1} + \mathbf{v} = \mathbf{w}$, the amplitudes of \mathbf{w} and \mathbf{v} differ only for the constant-mode. Let $\langle k,l \rangle \neq \langle 0,0 \rangle$. Then by (6.7)

$$\zeta_{k,l} = N^{-2} \sum_{t,r} w_{t,r} \exp(-i \frac{2\pi}{N} (kt + lr)) = N^{-2} \sum_{t,r} (1 + v_{t,r}) \exp(-i \frac{2\pi}{N} (kt + lr)).$$

As $w_{t,r} = 1 + v_{t,r} > 0$ for all $t,r \in Z_N$, we obtain

$$|\zeta_{k,l}| \leq N^{-2} \sum_{t,r} (1 + v_{t,r}) = 1 + N^{-2} \sum_{t,r} v_{t,r} = 1 + \zeta_{0,0}.$$

The approximation $\mathbf{v}_a = \mathbf{0}$.—By putting $\mathbf{v}_a = \mathbf{0}$ in (6.1) we obtain the following approximate differential equation for \mathbf{v}_p :

$$(6.10) \quad \dot{\mathbf{v}}_p = L(\mathbf{v}_p) + Q_p(\mathbf{v}_p) + K_p(\mathbf{v}_p).$$

We now give the different terms of it explicitly. The linear term is familiar from section 5 (see 5.8, 5.16):

$$(6.11) \quad L(\mathbf{v}_p) = \lambda(\zeta_{1,1} \mathbf{e}^{1,1} + \zeta_{-1,-1} \mathbf{e}^{-1,-1} + \zeta_{1,-1} \mathbf{e}^{1,-1} + \zeta_{-1,1} \mathbf{e}^{-1,1}).$$

The quadratic term (see 5.9) is obtained by evaluating $Q(\mathbf{v}_p)$ with the help of results of Section 5 and the property (6.5) for complex modes. Since all pairwise combinations of principal modes excite only the nine ancillary modes $\mathbf{e}^{0,0}$, $\mathbf{e}^{\pm 2, \pm 2}$, $\mathbf{e}^{\pm 2, 0}$ and $\mathbf{e}^{0, \pm 2}$ we have

$$(6.12) \quad Q_p(\mathbf{v}_p) = \mathbf{0}.$$

As we later will need also $Q_a(\mathbf{v}_p)$, let us give here the result:

$$(6.13) \quad Q_a(\mathbf{v}_p) = \\ = \gamma \zeta_{+1,+1} \zeta_{+1,+1} \mathbf{e}^{+2,+2} + \gamma \zeta_{-1,-1} \zeta_{-1,-1} \mathbf{e}^{-2,-2} \\ + \gamma \zeta_{+1,-1} \zeta_{+1,-1} \mathbf{e}^{+2,-2} + \gamma \zeta_{-1,+1} \zeta_{-1,+1} \mathbf{e}^{-2,+2} \\ + \gamma \zeta_{+1,+1} \zeta_{+1,-1} \mathbf{e}^{+2,0} + \gamma \zeta_{-1,-1} \zeta_{-1,+1} \mathbf{e}^{-2,0} \\ + \gamma \zeta_{+1,+1} \zeta_{-1,+1} \mathbf{e}^{0,+2} + \gamma \zeta_{-1,-1} \zeta_{+1,-1} \mathbf{e}^{0,-2}.$$

Note that these contributions are of second-order in the amplitudes of the principal modes; the growth-contribution to the constant-mode vanishes.)

The cubic term (5.10) contributes to $\dot{\mathbf{v}}_p$ as well as to $\dot{\mathbf{v}}_a$. Its contribution to the former is:

$$(6.14) \quad K_p(\mathbf{v}_p) =$$

$$\begin{aligned} & -\gamma(2\zeta_{+1,+1} \zeta_{-1,-1} + 4\zeta_{+1,-1} \zeta_{-1,+1}) \zeta_{+1,+1} \mathbf{e}^{+1,+1} \\ & -\gamma(2\zeta_{-1,-1} \zeta_{+1,+1} + 4\zeta_{-1,+1} \zeta_{+1,-1}) \zeta_{-1,-1} \mathbf{e}^{-1,-1} \\ & -\gamma(2\zeta_{+1,-1} \zeta_{-1,+1} + 4\zeta_{+1,+1} \zeta_{-1,-1}) \zeta_{+1,-1} \mathbf{e}^{+1,-1} \\ & -\gamma(2\zeta_{-1,+1} \zeta_{+1,-1} + 4\zeta_{-1,-1} \zeta_{+1,+1}) \zeta_{-1,+1} \mathbf{e}^{-1,+1}. \end{aligned}$$

By collecting the contributions for each principal mode we obtain the approximate system (6.15) for the four amplitudes $\zeta_{\pm 1, \pm 1}$ in its explicit form. Note that the principal modes interact only in third-order.

$$(6.15) \quad \begin{aligned} \zeta_{+1,+1} &= (\lambda - \gamma(2\zeta_{+1,+1} \zeta_{-1,-1} + 4\zeta_{+1,-1} \zeta_{-1,+1})) \zeta_{+1,+1}, \\ \zeta_{-1,-1} &= (\lambda - \gamma(2\zeta_{-1,-1} \zeta_{+1,+1} + 4\zeta_{-1,+1} \zeta_{+1,-1})) \zeta_{-1,-1}, \\ \zeta_{+1,-1} &= (\lambda - \gamma(2\zeta_{+1,-1} \zeta_{-1,+1} + 4\zeta_{+1,+1} \zeta_{-1,-1})) \zeta_{+1,-1}, \\ \zeta_{-1,+1} &= (\lambda - \gamma(2\zeta_{-1,+1} \zeta_{+1,-1} + 4\zeta_{-1,-1} \zeta_{+1,+1})) \zeta_{-1,+1}. \end{aligned}$$

This is an intermediate result. The more realistic adiabatic approximation will modify (6.15) by replacing the coefficients 2 and 4 by more complicated expressions.

Adiabatic approximation.—First, let us discuss the coupling between the components \mathbf{v}_p and \mathbf{v}_a in the differential equation (6.2). If \mathbf{v}_p is $\mathbf{0}$, then a small \mathbf{v}_a , damped by the linear term, is ‘attracted’ by $\mathbf{0}$. If \mathbf{v}_p is different from $\mathbf{0}$, the component \mathbf{v}_a is activated by the non-linear terms and the attractor point \mathbf{v}_c is given as solution of the equation

$$(6.16) \quad \mathbf{0} = L(\mathbf{v}_c) + Q_a(\mathbf{v}_p + \mathbf{v}_c) + K_a(\mathbf{v}_p + \mathbf{v}_c).$$

The regularity and the negative signs of all eigenvalues of L with respect to the ancillary modes secure at least in the neighbourhood of $\mathbf{0}$ the existence of an explicit solution $\mathbf{v}_c(\mathbf{v}_p)$ of (6.16) as well as the attractor property of $\mathbf{v}_c(\mathbf{v}_p)$. Since \mathbf{v}_c occurs also in the non-linear terms the uniqueness of this solution may be lost for large \mathbf{v}_p and also \mathbf{v}_c may lose its attractor property. Determining these limits turns out, however, to be very complicated and is beyond the scope of this paper.

If we choose the parameter α such that

$$(6.17) \quad |\lambda_a| \gg \lambda,$$

then \mathbf{v}_p and $\mathbf{v}_c(\mathbf{v}_p)$ will evolve very slowly in comparison with the relaxation time of \mathbf{v}_a . This means that the transient of $\mathbf{v}_a(0)$ towards $\mathbf{v}_c(\mathbf{v}_p)$ is of short duration and that \mathbf{v}_a will stay near to its attractor point, thus

$$(6.18) \quad \mathbf{v}_a \approx \mathbf{v}_c(\mathbf{v}_p).$$

As the time course of \mathbf{v}_a is controlled by \mathbf{v}_c , which in turn depends on that of \mathbf{v}_p ,

one speaks of a slaving of the ancillary component \mathbf{v}_a by the principal component \mathbf{v}_p by means of the control component $\mathbf{v}_c(\mathbf{v}_p)$.

By inserting $\mathbf{v}_c(\mathbf{v}_p)$ instead of \mathbf{v}_a into (6.1) we obtain the approximate differential equation for \mathbf{v}_p :

$$(6.19) \quad \dot{\mathbf{v}}_p = L(\mathbf{v}_p) + Q_p(\mathbf{v}_p + \mathbf{v}_c(\mathbf{v}_p)) + K(\mathbf{v}_p + \mathbf{v}_c(\mathbf{v}_p)).$$

Third-order approximation.—To obtain the differential equation (6.19) in more explicit form is still an involved problem as one has to solve the implicit equation (6.16) containing all ancillary modes. However, to gain insight into the system’s behaviour, an approximation of (6.19) up to third-order in the amplitudes $\zeta_{\pm 1, \pm 1}$ will eventually do. For this purpose it is sufficient to expand $\mathbf{v}_c(\mathbf{v}_p)$ up to second-order only. As $\mathbf{v}_c(\mathbf{0}) = \mathbf{0}$ and a first-order term would contradict (6.16), $\mathbf{v}_c(\mathbf{v}_p)$ is at least of second-order so that (6.16) reduces to

$$(6.20) \quad \mathbf{0} = L(\mathbf{v}_c) + Q_a(\mathbf{v}_p).$$

Hence with (6.20), (6.13) and (5.16) we obtain the second-order approximation for the control component $\mathbf{v}_c(\mathbf{v}_p)$, which is a superposition of eight ancillary modes.

$$(6.21) \quad \mathbf{v}_c(\mathbf{v}_p) =$$

$$\begin{aligned} & = \frac{\gamma}{-\lambda^{2,2}} \zeta_{+1,+1} \zeta_{+1,+1} \mathbf{e}^{+2,+2} + \frac{\gamma}{-\lambda^{-2,-2}} \zeta_{-1,-1} \zeta_{-1,-1} \mathbf{e}^{-2,-2} + \\ & + \frac{\gamma}{-\lambda^{2,-2}} \zeta_{+1,-1} \zeta_{+1,-1} \mathbf{e}^{+2,-2} + \frac{\gamma}{-\lambda^{-2,2}} \zeta_{-1,+1} \zeta_{-1,+1} \mathbf{e}^{-2,+2} + \\ & + \frac{\gamma}{-\lambda^{2,0}} \zeta_{+1,+1} \zeta_{+1,-1} \mathbf{e}^{+2,0} + \frac{\gamma}{-\lambda^{-2,0}} \zeta_{-1,-1} \zeta_{-1,+1} \mathbf{e}^{-2,0} + \\ & + \frac{\gamma}{-\lambda^{0,2}} \zeta_{+1,+1} \zeta_{-1,+1} \mathbf{e}^{0,+2} + \frac{\gamma}{-\lambda^{0,-2}} \zeta_{-1,-1} \zeta_{+1,-1} \mathbf{e}^{0,-2}. \end{aligned}$$

Let us return to (6.19). We have already given the contributions $L(\mathbf{v}_p)$, $Q_p(\mathbf{v}_p) = \mathbf{0}$, $K_p(\mathbf{v}_p)$ in (6.11), (6.12) and (6.14). The lowest order contributions of the control component are contained in $Q_p(\mathbf{v}_p + \mathbf{v}_c(\mathbf{v}_p))$ and are pairwise products of a principal mode and a mode of the control component. For example, some calculation based on results of section 5 shows that the additional contribution to the mode $\mathbf{e}^{+1,+1}$ consists of the six terms (similar contributions to the other principal modes can be obtained):

$$(6.22) \quad \left\{ \left(\frac{\gamma}{-\lambda^{2,2}} \zeta_{1,1} \zeta_{1,1} \right) \gamma \zeta_{-1,-1} + \left(\frac{\gamma}{-\lambda^{2,0}} \zeta_{1,1} \zeta_{1,-1} \right) \gamma \zeta_{-1,1} + \right.$$

$$\left. + \left(\frac{\gamma}{-\lambda^{0,2}} \zeta_{1,1} \zeta_{-1,1} \right) \gamma \zeta_{1,-1} + \zeta_{-1,-1} \gamma^{2,2} \left(\frac{\gamma}{-\lambda^{2,2}} \zeta_{1,1} \zeta_{1,1} \right) + \right.$$

$$\left. + \zeta_{-1,1} \frac{1}{2} \left(\gamma^{2,0} - 1 \right) \left(\frac{\gamma}{-\lambda^{2,0}} \zeta_{1,1} \zeta_{1,-1} \right) + \right.$$

$$\left. + \zeta_{1,-1} \frac{1}{2} \left(\gamma^{0,2} - 1 \right) \left(\frac{\gamma}{-\lambda^{0,2}} \zeta_{1,1} \zeta_{-1,1} \right) \right\} \mathbf{e}^{1,1}$$

$$= \gamma \left(\frac{\gamma + \gamma^{2,2}}{\alpha - \gamma^{2,2}} \zeta_{1,1} \zeta_{-1,-1} + \frac{\gamma + \frac{1}{2}(\gamma^{2,0} - 1)}{\alpha - \frac{1}{2}(\gamma^{2,0} - 1)} \zeta_{1,-1} \zeta_{-1,+1} + \frac{\gamma + \frac{1}{2}(\gamma^{0,2} - 1)}{\alpha - \frac{1}{2}(\gamma^{0,2} - 1)} \zeta_{1,-1} \zeta_{-1,1} \right) \zeta_{1,1} e^{1,1}.$$

The final system for the amplitudes of the principal modes in third-order approximation is:

$$\begin{aligned} \dot{\zeta}_{+1,+1} &= \left(\lambda - \gamma \left((2-a) \zeta_{+1,+1} \zeta_{-1,-1} + (4-b'-b'') \zeta_{+1,-1} \zeta_{-1,+1} \right) \right) \zeta_{+1,+1}, \\ \dot{\zeta}_{-1,-1} &= \left(\lambda - \gamma \left((2-a) \zeta_{-1,-1} \zeta_{+1,+1} + (4-b'-b'') \zeta_{-1,+1} \zeta_{+1,-1} \right) \right) \zeta_{-1,-1}, \end{aligned} \quad (6.23)$$

$$\begin{aligned} \dot{\zeta}_{+1,-1} &= \left(\lambda - \gamma \left((2-a) \zeta_{+1,-1} \zeta_{-1,+1} + (4-b'-b'') \zeta_{+1,+1} \zeta_{-1,-1} \right) \right) \zeta_{+1,-1}, \\ \dot{\zeta}_{-1,+1} &= \left(\lambda - \gamma \left((2-a) \zeta_{-1,+1} \zeta_{+1,-1} + (4-b'-b'') \zeta_{-1,-1} \zeta_{+1,+1} \right) \right) \zeta_{-1,+1}, \end{aligned}$$

$$(6.24) \quad \text{with } a = \frac{\gamma + \gamma^{\pm 2, \pm 2}}{\alpha - \gamma^{\pm 2, \pm 2}}, \quad b' = \frac{\gamma + \frac{1}{2}(\gamma^{\pm 2, 0} - 1)}{\alpha - \frac{1}{2}(\gamma^{\pm 2, 0} - 1)}, \quad b'' = \frac{\gamma + \frac{1}{2}(\gamma^{0, \pm 2} - 1)}{\alpha - \frac{1}{2}(\gamma^{0, \pm 2} - 1)}$$

Whether the approximation (6.23) efficiently fits the evolution of the principal component depends on the numerical values of all coefficients of the system and will not be investigated here. Notice that especially the amplitudes in the control component (6.21) can become very large and thus can invalidate the approximation in the region of interest given by (6.9). We will now discuss the evolution according to (6.23) of the principal component, which depends on some eigenvalues of C only and the parameter a .

Transformation to real modes.—Let us expand \mathbf{v}_p in the basis of real modes:

$$(6.25) \quad \mathbf{v}_p = \xi_c \mathbf{c}^{1,1} + \xi_s \mathbf{s}^{1,1} + \eta_c \mathbf{c}^{1,-1} + \eta_s \mathbf{s}^{1,-1}.$$

The transformation of coordinates is given by

$$\begin{aligned} \zeta_{+1,+1} &= \frac{1}{2} (\xi_c - i \xi_s), \quad \xi_c = \zeta_{+1,+1} + \zeta_{-1,-1}, \\ \zeta_{-1,-1} &= \frac{1}{2} (\xi_c + i \xi_s), \quad \xi_s = i(\zeta_{+1,+1} - \zeta_{-1,-1}), \end{aligned}$$

$$(6.26) \quad \begin{aligned} \zeta_{+1,-1} &= \frac{1}{2} (\eta_c - i \eta_s), \quad \eta_c = \zeta_{+1,-1} + \zeta_{-1,+1}, \\ \zeta_{-1,+1} &= \frac{1}{2} (\eta_c + i \eta_s), \quad \eta_s = i(\zeta_{+1,-1} - \zeta_{-1,+1}). \end{aligned}$$

With the identities

$$\zeta_{+1,+1} \zeta_{-1,-1} = \frac{1}{4} (\xi_c^2 + \xi_s^2) \quad \text{and} \quad \zeta_{+1,-1} \zeta_{-1,+1} = \frac{1}{4} (\eta_c^2 + \eta_s^2) \quad \text{the system (6.23)}$$

becomes:

$$(6.27) \quad \begin{aligned} \dot{\xi}_c &= \left(\lambda - \frac{\gamma}{4} \left((2-a) (\xi_c^2 + \xi_s^2) + (4-b'-b'') (\eta_c^2 + \eta_s^2) \right) \right) \xi_c, \\ \dot{\xi}_s &= \left(\lambda - \frac{\gamma}{4} \left((2-a) (\xi_c^2 + \xi_s^2) + (4-b'-b'') (\eta_c^2 + \eta_s^2) \right) \right) \xi_s, \\ \dot{\eta}_c &= \left(\lambda - \frac{\gamma}{4} \left((2-a) (\eta_c^2 + \eta_s^2) + (4-b'-b'') (\xi_c^2 + \xi_s^2) \right) \right) \eta_c, \\ \dot{\eta}_s &= \left(\lambda - \frac{\gamma}{4} \left((2-a) (\eta_c^2 + \eta_s^2) + (4-b'-b'') (\xi_c^2 + \xi_s^2) \right) \right) \eta_s. \end{aligned}$$

As only real deviations are of interest, ξ_c , ξ_s , η_c and η_s may be considered as real.

The terms $2-a$ and $4-b'-b''$.—The behaviour of the evolution according to (6.27) depends on the signs of these two terms and their relative sizes. To investigate these terms, let us recall some facts shown in Section 5. We have $0 < \gamma \leq 1$, $-\gamma < \gamma^{\pm 2, \pm 2} < \gamma$, $-1 \leq \gamma^{\pm 2, 0} \leq 1$, $-1 \leq \gamma^{0, \pm 2} \leq 1$ and $\gamma^{\pm 2, \pm 2} = \gamma^{\pm 2, 0} \cdot \gamma^{0, \pm 2}$. The choice of a according to linear analysis is such that $\lambda = -\alpha + \gamma > 0$ and $\lambda^{\pm 2, \pm 2} = -\alpha + \gamma^{\pm 2, \pm 2} < 0$, thus $\gamma^{\pm 2, \pm 2} < \alpha < \gamma$. As λ is assumed to be only slightly positive, the assumption $0 < \alpha < \gamma$ (i.e. $\lambda/\alpha < 1$) is no serious further restriction.

The discussion of the function $(\gamma+x)/(a-x)$ gives, for the coefficients a , b' and b'' , the following results which are of relevance here:

Concerning a ,

$$\text{if } \left\{ \begin{array}{l} -\gamma < \gamma^{\pm 2, \pm 2} < 0, \\ 0 \leq \gamma^{\pm 2, \pm 2} < (2\alpha - \gamma)/3 \text{ or} \\ (2\alpha - \gamma)/3 \leq \gamma^{\pm 2, \pm 2} < \alpha, \end{array} \right\} \quad \text{then } \left\{ \begin{array}{l} 0 < a < \gamma/\alpha, \\ \gamma/\alpha \leq a < 2 \text{ or} \\ 2 \leq a < \infty, \end{array} \right\} \quad \text{respectively.}$$

Concerning b', b'' , we have $b', b'' \leq \gamma/\alpha$, since both $\frac{1}{2}(\gamma^{\pm 2, 0} - 1)$

and $\frac{1}{2}(\gamma^{0, \pm 2} - 1)$ are negative.

The term $4-b'-b''$ is positive, since $\gamma/\alpha = 1 + \lambda/\alpha < 2$. The positiveness of $2-a$ is secured as long as a can be chosen such that $\gamma^{\pm 2, \pm 2} < (2\alpha - \gamma)/3$. This, however, is only possible if $\gamma^{\pm 2, \pm 2} < \gamma/3$, as $(2\alpha - \gamma)/3 = \gamma/3 - 2\lambda/3$.

Comparison of the coefficients shows that $4 - b' - b'' > 2 - a$. The proof is obvious if $\gamma^{\pm 2, \pm 2} \geq 0$. For $\gamma^{\pm 2, \pm 2} < 0$, we make use of the fact that one of the eigenvalues $\gamma^{\pm 2, 0}$, $\gamma^{0, \pm 2}$ is negative, giving for one of the coefficients b' or b'' an upper bound $(\gamma - 1/2)/(a + 1/2)$ which is smaller than the one given above.

Discussion of (6.27).—At any moment, the principal component v_p is a superposition of two (broken) diagonal-modes with different orientation. Their amplitudes are

$$\xi = + \sqrt{\xi_c^2 + \xi_s^2} \quad \text{and} \quad \eta = + \sqrt{\eta_c^2 + \eta_s^2}$$

and their phase-shift angles are given by the ratios

$$\xi_c: \xi_s \quad \text{and} \quad \eta_c: \eta_s.$$

Since these ratios stay constant according to (6.27) the equations can be reduced to a system in ξ and η only:

$$(6.28) \quad \begin{aligned} \dot{\xi} &= \left(\lambda - \frac{\gamma}{4} \left((2-a) \xi^2 + (4-b'-b'') \eta^2 \right) \right) \xi, \\ \dot{\eta} &= \left(\lambda - \frac{\gamma}{4} \left((2-a) \eta^2 + (4-b'-b'') \xi^2 \right) \right) \eta. \end{aligned}$$

For small values the two amplitudes grow independently of each other with the same rate coefficient λ . Gradually these coefficients are modified by the third-order terms, and interactions take place. Since $4 - b' - b'' > 2 - a$ the two amplitudes compete: The one of the them which is slightly larger than the other also has an advantage in its rate-coefficient. Furthermore, if $\gamma^{\pm 2, \pm 2} < (2a - \gamma)/3$, then ξ and η are both bounded in their evolution, since $2 - a$, $4 - b' - b''$ are both positive. This leads to selection of one of the amplitudes with the final stationary value $2\sqrt{\lambda/\gamma(2-a)}$. Although (6.27, 6.28) correctly describe the system's qualitative behaviour, the explicit value of the final amplitude has to be considered with caution. In case $\gamma^{\pm 2, \pm 2}$ is slightly below $(2a - \gamma)/3$, the value $2 - a$ is very small and the above expression correspondingly very large. It may even exceed the absolute bounds (see 6.9) imposed by the original equations. If $\gamma/3 \leq \gamma^{\pm 2, \pm 2}$, then any choice of a will lead to a negative value for $2 - a$, thus the third-order approximation does not even qualitatively give existence of bounds. An approximation to higher order has then to be considered.

It is of great help in the discussion of (6.28) to realize that it can be written in the form $\dot{\xi} = -\partial V/\partial \xi$, $\dot{\eta} = -\partial V/\partial \eta$ with the potential (see Fig. 8).

$$(6.29) \quad \begin{aligned} V(\xi, \eta) &= \\ &= -\frac{\lambda}{2} (\xi^2 + \eta^2) + \frac{\gamma}{16} \left((2-a) (\xi^4 + \eta^4) + 2(4-b'-b'') \xi^2 \eta^2 \right) \\ &= -\frac{\lambda}{2} (\xi^2 + \eta^2) + \frac{\gamma}{16} (2-a) (\xi^2 + \eta^2)^2 + \frac{\gamma}{8} (2+a-b'-b'') \xi^2 \eta^2. \end{aligned}$$

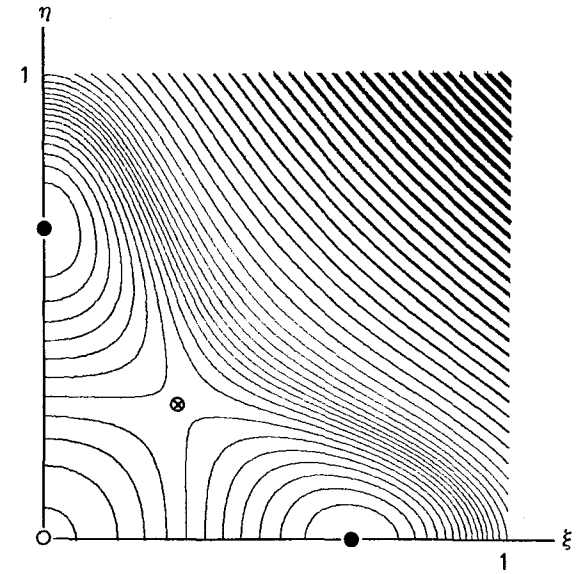


Fig. 8. In the linear approximation the diagonal-mode components of the deviation v grow independently of each other with the same rate-coefficient $\lambda = -a + \gamma$. Interactions between all modes are described by the full set of differential equations; in particular the two diagonal-modes compete with each other. The adiabatic elimination of the ancillary modes (i.e. the damped ones) leads to the differential equations $\dot{\xi} = -\partial V/\partial \xi$, $\dot{\eta} = -\partial V/\partial \eta$ for the amplitudes ξ and η of the two diagonal-mode components with a potential $V(\xi, \eta)$ of fourth degree. The figure shows equipotential curves of $V(\xi, \eta)$, the local maximum \circ in the origin, the saddle point \otimes on the bisector $\xi = \eta$ and the two minima \bullet on the axes. If one of the amplitudes is favoured in the initial configuration, the corresponding diagonal-mode component will be selected during the system's evolution.

(In the second version, the first two terms are symmetric under rotation.)

Conclusion.—Let $w(0)$ be an initial configuration in the neighbourhood of $\mathbf{1}$ at time zero. If the deviation $v(0) = w(0) - \mathbf{1}$ contains a principal component of the following type

$$(6.30) \quad v_p(0) = \xi_c(0)c^{1,1} + \xi_s(0)s^{1,1} + \eta(0)c^{1,-1}$$

with $\eta(0) > \xi(0) = \sqrt{\xi_c^2(0) + \xi_s^2(0)}$, then the above third-order analysis shows that the evolution of v_p converges toward the diagonal-mode $2\sqrt{\lambda/\gamma(2-a)} c^{1,-1}$ (note that the cyclic symmetry is broken only by the lack of a $s^{1,-1}$ component in the initial configuration). In addition to this evolution of v_p , we obtain by (6.21) the control component $v_c(v_p)$ which is the attractor for the ancillary component v_a during evolution. In particular, an approximate final configuration of weights is given by

$$(6.31) \quad 1 + 2\sqrt{\lambda/\gamma(2-a)} c^{1,-1} + 2\frac{\gamma}{-\lambda^2 - 2} (\lambda/\gamma(2-a)) c^{2,-2},$$

in which the second harmonic, resulting from (6.21), helps to sharpen the shape of the diagonal-mode.

7. Explicit calculation of the final configuration

The shape of the approximate final configuration (6.31), although containing a second harmonic as component, is very broad. To show that the final configuration is much narrower, higher order approximations have to be considered. For this purpose the control component $v_c(v_p)$ has to be calculated to more than second-order (note that in contrast to the implicit equation (6.16), which is only cubic, the explicit expression for $v_c(v_p)$ may be of higher order). Since after selection the principal component v_p consists of one diagonal-mode only, e.g. $\eta c^{1,-1} = \eta/2 e^{1,-1} + \eta/2 e^{-1,1}$, the control component $v_c(\eta c^{1,-1})$ will contain only the modes of the form $c^{k,-k}$, $k \neq \pm 1$, which are produced as powers of $c^{1,-1}$. Thus, $c^{1,-1}$ slaves only those higher cosine harmonics which contribute to narrow the shape of the selected diagonal. Equivalently and more directly the original differential equations (5.6) are investigated with the ansatz

$$(7.1) \quad \mathbf{w} = \sum_k \zeta_k e^{k,-k}.$$

As \mathbf{w} is supposed to be real, we have $\zeta_k = \bar{\zeta}_{-k}$. Reduction to harmonics $c^{k,-k}$, $k \in Z_N$, will be obtained by $\zeta_k = \zeta_{-k}$ (or $\zeta_k \in \mathbb{R}$). The connection between (7.1) and the expansion (6.4) is established by the equivalences $\zeta_0 \equiv 1 + \zeta_{0,0}$ and $\zeta_k \equiv \zeta_{k,-k}$, $k \neq 0$.

Since \mathbf{w} as well as $\mathbf{w} \cdot C(\mathbf{w})$ contain neither column nor row modes, we have

$$(7.2) \quad B(\mathbf{w}) = \zeta_0 \mathbf{1}$$

and with the definition

$$(7.3) \quad p(\mathbf{w}) = \sum_j \zeta_{-j} \zeta_j \gamma^{j,-j},$$

we obtain

$$(7.4) \quad B(\mathbf{w} \cdot C(\mathbf{w})) = p(\mathbf{w}) \mathbf{1}.$$

In short, B projects onto the constant-mode component of \mathbf{w} as well as of $\mathbf{w} \cdot C(\mathbf{w})$. Since these configurations are positive throughout development, we have

$$(7.5) \quad 0 < \zeta_0 \text{ and } 0 < p(\mathbf{w}).$$

Furthermore, with (6.9), we have bounds for the amplitudes:

$$(7.6) \quad |\zeta_k| < \zeta_0 \text{ for } k \in Z_N.$$

With (7.4) the differential equation (5.6), specialized for the ansatz (7.1), reduces to ($\beta = 1$):

$$(7.7) \quad \dot{\mathbf{w}} = -\alpha(\mathbf{w} - \mathbf{1}) + \mathbf{w} \cdot C(\mathbf{w}) - p(\mathbf{w}) \mathbf{w}.$$

If we insert (7.1), we obtain by comparison of terms

$$(7.8) \quad \begin{aligned} \dot{\zeta}_0 &= -(\alpha + p(\mathbf{w})) (\zeta_0 - 1), \\ \dot{\zeta}_k &= -(\alpha + p(\mathbf{w})) \zeta_k + \sum_j \zeta_{k-j} \zeta_j \gamma^{j,-j}, \quad k \neq 0. \end{aligned}$$

Since $\alpha + p(\mathbf{w})$ is positive, equation (7.8) shows that the constant-mode contribution $\zeta_0 \mathbf{1}$ converges to $\mathbf{1}$. We therefore put $\zeta_0 = 1$ from now on.

In the following explicit calculations we restrict ourselves to the special case

$$(7.9) \quad \begin{aligned} c_T(m) &= \frac{1}{N} (1 + 2\gamma_T \cos(\frac{2\pi}{N} m)), \\ c_R(n) &= \frac{1}{N} (1 + 2\gamma_R \cos(\frac{2\pi}{N} n)), \end{aligned}$$

with $0 < \gamma_T, \gamma_R < \frac{1}{2}$.

The eigenvalues of the operator C are given by (5.23). In particular we have $\gamma^{0,0} = 1$, $\gamma = \gamma^{1,-1} = \gamma^{-1,1} = \gamma_T$, $\gamma_R > 0$, and $\gamma^{j,-j} = 0$ otherwise.

The differential equations (7.8) now reduce to

$$(7.10) \quad \begin{aligned} \dot{\zeta}_0 &= 1, \\ \dot{\zeta}_k &= -(\alpha + 2\gamma \zeta_1 \zeta_{-1}) \zeta_k + \gamma(\zeta_1 \zeta_{k-1} + \zeta_{-1} \zeta_{k+1}), \quad k \neq 0. \end{aligned}$$

For a stationary solution containing higher cosine harmonics only, in which we are interested here, we have to solve the equations

$$(7.11) \quad \begin{aligned} \zeta_0 &= \zeta_N = 1; \\ \zeta_k &= \zeta_{N-k}, \quad 0 \leq k \leq N; \\ \zeta_k &= \frac{\gamma \zeta_1}{\alpha + 2\gamma \zeta_1^2} (\zeta_{k-1} + \zeta_{k+1}), \quad 0 < k < N. \end{aligned}$$

These equations have as solution a gravitating chain, suspended between the points $\zeta_0 = \zeta_N = 1$. The general symmetric form of such a discrete chain is

$$(7.12) \quad \zeta_k(\varepsilon) = \frac{\varepsilon^k + \varepsilon^{N-k}}{1 + \varepsilon^N}, \quad 0 \leq k \leq N.$$

These values satisfy

$$(7.13) \quad \begin{aligned} \zeta_0(\varepsilon) &= \zeta_N(\varepsilon) = 1; \\ \zeta_k(\varepsilon) &= \zeta_{N-k}(\varepsilon), \quad 0 \leq k \leq N; \\ \zeta_k(\varepsilon) &= \frac{\varepsilon}{\varepsilon^2 + 1} (\zeta_{k-1}(\varepsilon) + \zeta_{k+1}(\varepsilon)), \quad 0 < k < N. \end{aligned}$$

The configuration w_ε with these amplitudes is

$$(7.14) \quad w_\varepsilon = \sum_k \zeta_k(\varepsilon) e^{k-k} = \sum_k \zeta_k(\varepsilon) e^{k-k}.$$

If $\varepsilon=0$, then only the constant-mode contributes, i.e. $w_0=1$. If $\varepsilon=1$, then all amplitudes are 1. The resulting configuration w_1 has on the diagonal the weights N and is otherwise zero. For $0<\varepsilon<1$, we obtain the weights of the retinal fibre $r=0$ by summation as

$$(7.15) \quad w_{t,0} = \frac{1+\varepsilon}{1+\varepsilon^N} \frac{(1-\varepsilon^N)(1-\varepsilon)}{1-2\varepsilon \cos\left(\frac{2\pi}{N}t\right)+\varepsilon^2}, \quad t \in \mathbb{Z}_N.$$

In particular

$$(7.16) \quad w_{0,0} = \frac{1+\varepsilon}{1+\varepsilon^N} \cdot \frac{1-\varepsilon^N}{1-\varepsilon}, \quad \text{the maximal weight,}$$

$$(7.17) \quad w_{N/2,0} = \frac{1-\varepsilon^N}{1+\varepsilon^N} \cdot \frac{1-\varepsilon}{1+\varepsilon}, \quad \text{the minimal weight.}$$

We are now left with the problem of finding ε such that $\zeta_k(\varepsilon)$, $0 \leq k \leq N$, satisfies the equations of (7.11) determined by α and γ . It suffices to compare the coefficients and the first value:

$$(7.18) \quad \frac{\gamma \zeta_1}{\alpha + 2\gamma \zeta_1^2} = \frac{\varepsilon}{\varepsilon^2 + 1}$$

$$(7.19) \quad \zeta_1 = \zeta_1(\varepsilon).$$

An approximate solution is

$$(7.20) \quad \varepsilon \cong \sqrt{(-\alpha + \gamma)/\gamma} = \sqrt{\lambda/\gamma}.$$

Since $\lambda = -\alpha + \gamma > 0$ and $\alpha > 0$, we have $0 < \alpha < \gamma$ and hence $0 < \varepsilon < 1$. The cases $\alpha = \gamma$ ($\lambda = 0$), $\alpha = 0$ ($\lambda = \gamma$) lead to the configurations w_ε with $\varepsilon = 0$ and $\varepsilon = 1$ respectively (see Fig. 9).

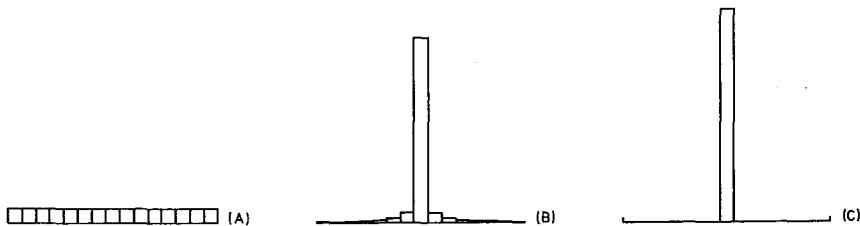


Fig. 9. Three final configurations for different choices of α . Each histogram illustrates the connection-weights of a single retinal fibre. (A) $\alpha = \gamma$ (or $\lambda = 0$) leads to the homogeneous solution. (B) $0 < \alpha < \gamma$ (or $0 < \sqrt{\lambda/\gamma} < 1$), a retinal fibre projects on a small region on the tectum. (C) $\alpha = 0$ (or $\lambda = \gamma$), the precise retinotopic projection.

Upon a gradual decrease of the parameter α to zero, the selected diagonal-mode component activates precisely those of the ancillary modes which can contribute to its narrowing.

Conclusion.—Due to the fact that the selected diagonal-mode component slaves its higher cosine harmonics by the non-linear terms, the shape of the final configuration can be very narrow. If the parameter α is gradually decreased after selection has taken place, the shape even approaches the extreme case of a one-to-one retinotopic projection (at $\alpha = 0$).

Acknowledgement

We would like to thank Professor E. Ruch for motivation and encouragement. This investigation represents a first result in the context of a broader effort, initiated by Professor Ruch, to clarify the phenomena of organization.

References

- Gaze, R. M. (1978). The problem of specificity in the formation of nerve connections. In: *Specificity of Embryological Interactions* (D. Garrod, Ed.). Chapman and Hall, London.
- Haken, H. (1978). *Synergetics, Introduction*. Springer-Verlag, Berlin, Heidelberg, New York.
- Haken, H. (1975a). Generalized Ginsburg-Landau Equations for Phase Transition-like Phenomena in Lasers, Nonlinear Optics, Hydrodynamics and Chemical Reactions. *Z. Physik B* 21, 105-114.
- Haken, H. (1975b). Higher Order Corrections to Generalized Ginsburg-Landau Equations of Non-Equilibrium Systems. *Z. Physik B* 22, 69-72.
- Turing, A. M. (1952). The chemical basis of morphogenesis. *Philos. Trans. R. Soc. London, Ser. B* 237, 37-72.
- von der Malsburg, C. and Willshaw, D. J. (1977). How to label nerve cells so that they can interconnect in an ordered fashion. *Proc. Natl. Acad. Sci. U.S.A.* 74, 5176-5178.
- von der Malsburg, C. and Willshaw, D. J. (1981). Differential equations for the development of topological nerve fibre projections. In: *Mathematical Psychology and Psychophysiology* (S. Grossberg, Ed.). *SIAM-AMS Proc.* 13 39-47
- von der Malsburg, C. (1981). The Correlation Theory of Brain Function. *Internal Report 81-2*, Department of Neurobiology, Max-Planck-Institute for Biophysical Chemistry, D-3400 Göttingen, West Germany.
- Willshaw, D. J. and von der Malsburg, C. (1979). A marker induction mechanism for the establishment of ordered neural mappings: its application to the retinotectal problem. *Philos. Trans. R. Soc. London, Ser. B* 287, 203-243.