Oscillatory Cortical Activity during Visual Hallucinations

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Abstract. From a theoretical point of view we investigate cortical activity patterns causing dynamical visual hallucinations. For this reason we analyze an oscillatory instability of the dynamics of the activator-inhibitor model of Ermentrout and Cowan. Such an oscillatory instability occurs as a result of several disease mechanisms. We explicitly derive the order parameter equation. By means of the averaging theorem, we obtain the averaged order parameter equation. The latter enables us to determine stable and unstable bifurcating cortical activity patterns analytically in lowest order. Depending on model parameters as well as on initial conditions two types of cortical activity patterns occur: travelling waves and ‘blinking rolls’, i.e. standing waves oscillating with the same frequency and with a phase shift of $\pi/2$. In contrast to cortical activity patterns caused by non-oscillatory instabilities analyzed by Ermentrout and Cowan (1979) and by the author (1995) the travelling waves and the blinking rolls lead to a variety of *dynamical* visual hallucinations which are discussed in detail.

Key words: Activator–inhibitor network, Pattern formation, Bifurcation, Center manifold, Order parameter equation, Blinking rolls, Visual hallucinations

1. Introduction

Pattern formation of brain activity is of great current interest [12]. In order to study cortical activity patterns causing visual hallucinations, Ermentrout and Cowan presented a paradigmatic activator–inhibitor model derived by means of only a few neurophysiologically motivated assumptions [6]. Field variables, activator and inhibitor, describe the activities of excitatory and inhibitory neurons on a macroscopic level.

Ermentrout and Cowan studied the geometrical properties of the bifurcating activity patterns caused by a non-oscillatory instability [6]. Another non-oscillatory instability was investigated by the author [24]. The bifurcating activity patterns caused by these non-oscillatory instabilities are *static* spatial patterns, for instance plane waves and hexagonal patterns [6, 24]. According to the visuo-cortical transformation [4, cf. 5] these patterns of cortical activity cause *static* visual hallucinations, such as static spiral, tunnel, and funnel hallucinations [6, 24].

In contrast to the study of Ermentrout and Cowan [6] and to a former study of the author [24] this article is devoted to the analysis of an *oscillatory instability* of the dynamics of the Ermentrout and Cowan model. Such an oscillatory instability

occurs as a consequence of a variety of disease mechanisms provided the mutual interactions of activator and inhibitor are strong enough. This will be discussed below in detail.

In order to analyze the dynamics of the emerging activity patterns we use the slaving principle of synergetics [9, 10]. The mathematical formulation of the slaving principle is guaranteed by the existence of a center manifold [15, 20]. This approach enables us to approximate the dynamics of the system in a neighborhood of the oscillatory instability by the reduced problem which is a low dimensional equation called *order parameter equation* [9, 10, 15, 20].

As a consequence of the oscillatory instability the dynamics of the order parameters act on two time scales: fast variables cause a ‘tremor’ of slowly varying amplitudes. This tremor is extracted by applying the *averaging theorem* (cf. Thm 4.1.1 in [8], Thm 3.2 in [13], ch. 4 in [1]). Consequently we end up with the averaged order parameter equation which is analyzed analytically. Depending on the model’s parameters one, four or eight complex pairs of eigenvalues cross the imaginary axis. Due to symmetry properties this gives rise to a single-mode, a four-modes or an eight-modes instability. In all three cases the dynamics of the averaged system is investigated analytically as well as numerically. The bifurcating activity patterns are determined analytically in lowest order. This enables us to investigate the corresponding visual hallucinations in detail.

The paper is organized as follows. The well-known model of Ermentrout and Cowan [6] is briefly sketched in Section 2. Section 3 is devoted to the linear problem. The disease mechanisms causing an oscillatory instability are presented in Section 4. The order parameter equation is derived and analyzed in Section 5. Numerical simulations of the order parameter equations as well as plots of the bifurcating activity patterns and the corresponding visual hallucinations are presented in Section 6. Finally we discuss our results in Section 7. Some mathematical details are presented in the appendix.

2. The Model of Ermentrout and Cowan

In the model of Ermentrout and Cowan [6] two neuronal populations, the excitatory neurons and the inhibitory neurons, are interacting by means of excitatory as well as inhibitory radially isotropic long-range interactions. In comparison to the recurrent positive interactions the lateral interactions of negative feedback type dominate. Let us denote the (time course grained) firing rates of the excitatory and inhibitory neurons at point $\mathbf{x}$ at time t by $E(\mathbf{x}, t)$ and $I(\mathbf{x}, t)$. The model of Ermentrout and Cowan [6] reads

$$\frac{\partial E}{\partial t} = -E + S_E(\alpha_{EE}w_{EE} * E - \alpha_{IE}w_{IE} * I), \quad (1)$$

$$\frac{\partial I}{\partial t} = -I + S_I(\alpha_{EI}w_{EI} * E - \alpha_{II}w_{II} * I). \quad (2)$$

$w_{EE}, w_{EI}, w_{IE}, w_{II}$ are Gaussian functions modeling the long-range neuronal interactions. $w * g$ denotes the double convolution given by

$$w * g = \int_{-\pi}^{\pi} \int_{-\pi}^{\pi} w(\mathbf{x} - \mathbf{x}') g(\mathbf{x}') dx'_1 dx'_2. \quad (3)$$

$\alpha_{EE}, \alpha_{EI}, \alpha_{IE}, \alpha_{II}$ are positive constants corresponding to the strength of the long-range neuronal interactions. S_E and S_I are the characteristic output functions of the excitatory and inhibitory cells, satisfying:

- (1) S_E and S_I are nondecreasing;
- (2) $S_E(\xi)$ and $S_I(\xi)$ are bounded as $\xi \rightarrow \pm \infty$;
- (3) S_E and S_I have unique inflection points (thresholds).

By putting $\alpha_{EE} \rightarrow \alpha_{EE} \lambda$ and $\alpha_{EI} \rightarrow \alpha_{EI} \lambda$, Ermentrout and Cowan introduced a parameter, λ , which modulates the excitability of the network. Starting at the resting state, i.e., $E = I = 0$, and increasing λ , they analyzed the linear stability of the resting state. Ermentrout and Cowan restricted the solution space to the class of doubly periodic functions. They analyzed the unstable modes in great detail. They also assumed that only one real eigenvalue crosses the imaginary axis. They did not derive an order parameter equation explicitly. For further information we refer the reader to Ermentrout and Cowan [6].

3. Linear Problem

In the present paper we analyze an *oscillatory instability* of the model of Ermentrout and Cowan. Such an instability gives rise to activity patterns which are qualitatively different in comparison to those analyzed by Ermentrout and Cowan [6] and to those analyzed by the author [24]. An oscillatory instability may be caused by several mechanisms. In order to discuss them we first have to investigate the linear problem of the model Equations (1) and (2). To this end we carry out a Fourier transformation of Equations (1) and (2). This enables us to determine the spectrum of the linear problem.

The double periodicity of the model allows us to expand $E(\mathbf{x}, t)$ and $I(\mathbf{x}, t)$ in terms of Fourier modes:

$$E(\mathbf{x}, t) = \sum_{\mathbf{k} \in \mathbb{Z}^2} \hat{E}(\mathbf{k}, t) e^{i\mathbf{k} \cdot \mathbf{x}} \quad \text{and} \quad I(\mathbf{x}, t) = \sum_{\mathbf{k} \in \mathbb{Z}^2} \hat{I}(\mathbf{k}, t) e^{i\mathbf{k} \cdot \mathbf{x}}, \quad (4)$$

where $\mathbf{k} = (k_1, k_2)$ denotes a wave vector. The sums in Equation (4) run over all integer k_1 and k_2 . The scalar product of the vectors $\mathbf{k}$ and $\mathbf{x}$ is denoted by $\mathbf{k} \cdot \mathbf{x}$.

With a little calculation we obtain the linear part of the Fourier transformed system:

$$\frac{d}{dt} \begin{pmatrix} \hat{E}(\mathbf{k}, t) \\ \hat{I}(\mathbf{k}, t) \end{pmatrix} = B(\mathbf{k}) \begin{pmatrix} \hat{E}(\mathbf{k}, t) \\ \hat{I}(\mathbf{k}, t) \end{pmatrix}, \quad (5)$$

for all $\mathbf{k} = (k_1, k_2)$ with integer k_1 and k_2 . The matrix of the linear operator of the wave vector $\mathbf{k}$ reads

$$B(\mathbf{k}) = \begin{pmatrix} a(\mathbf{k}) & b(\mathbf{k}) \\ c(\mathbf{k}) & d(\mathbf{k}) \end{pmatrix}, \quad (6)$$

where

$$a(\mathbf{k}) = -1 + S'_E(0)\alpha_{EE}\hat{w}_{EE}(\mathbf{k}), \quad b(\mathbf{k}) = -S'_E(0)\alpha_{IE}\hat{w}_{IE}(\mathbf{k}), \quad (7)$$

$$c(\mathbf{k}) = S'_I(0)\alpha_{EI}\hat{w}_{EI}(\mathbf{k}), \quad d(\mathbf{k}) = -1 - S'_I(0)\alpha_{II}\hat{w}_{II}(\mathbf{k}). \quad (8)$$

In order to analyze the spectrum of the linear problem we consider the characteristic equation for each wave vector $\mathbf{k}$:

$$\det(B(\mathbf{k}) - \lambda I) = \lambda^2 - (a(\mathbf{k}) + d(\mathbf{k}))\lambda + a(\mathbf{k})d(\mathbf{k}) - b(\mathbf{k})c(\mathbf{k}) = 0. \quad (9)$$

I denotes the identity matrix. We profit from the symmetry properties of w_{EE} , w_{EI} , w_{IE} , and w_{II} which were analyzed in detail in [24]. As a consequence of these symmetry properties the identities

$$\begin{aligned} \hat{w}(k_1, k_2) &= \hat{w}(k_2, -k_1) = \hat{w}(-k_1, -k_2) = \hat{w}(-k_2, k_1) \\ &= \hat{w}(k_2, k_1) = \hat{w}(k_1, -k_2) = \hat{w}(-k_2, -k_1) \\ &= \hat{w}(-k_1, k_2), \end{aligned} \quad (10)$$

hold for all integer k_1 and k_2 . Due to these relations all coefficients of the characteristic Equation (9) are real. This was shown in [24].

3.1 TYPES OF INSTABILITY

With Equation (9) we immediately obtain the eigenvalues of $B(\mathbf{k})$:

$$\lambda_{1,2}(\mathbf{k}) = -1 + \frac{1}{2}[S'_E(0)\alpha_{EE}\hat{w}_{EE}(\mathbf{k}) - S'_I(0)\alpha_{II}\hat{w}_{II}(\mathbf{k})] \pm \sqrt{\Delta(\mathbf{k})}, \quad (11)$$

with

$$\begin{aligned} \Delta(\mathbf{k}) &= [S'_E(0)\alpha_{EE}\hat{w}_{EE}(\mathbf{k}) + S'_I(0)\alpha_{II}\hat{w}_{II}(\mathbf{k})]^2 \\ &\quad - 4S'_E(0)S'_I(0)\alpha_{EI}\alpha_{IE}\hat{w}_{EI}(\mathbf{k})\hat{w}_{IE}(\mathbf{k}). \end{aligned} \quad (12)$$

Starting at the stable resting state, i.e. $E = I = 0$, one or several of the parameters α_{EE} , α_{EI} , α_{IE} , and α_{II} are varied so that for at least one wave vector $\mathbf{k}$ one or two eigenvalues cross the imaginary axis. In order to investigate the type of instability let us write Equation (11) in the form

$$\lambda_{1,2}(\mathbf{k}) = \Gamma(\mathbf{k}; \{\eta\}) \pm \sqrt{\Delta(\mathbf{k}; \{\eta\})}, \quad (13)$$

where $\{\eta\}$ denotes the control parameters, i.e. those of the parameters α_{EE} , α_{EI} , α_{IE} , and α_{II} which are varied. Let us assume that the control parameters finally reach critical values (denoted by $\{\eta\}_{\text{crit}}$) giving rise to an instability. There are three different possibilities:

- (1) $\Delta(\mathbf{k}; \{\eta\}_{\text{crit}}) > 0$: A single real eigenvalue (of the wave vector $\mathbf{k}$) crosses the imaginary axis: $\text{Re}(\lambda_1(\mathbf{k}; \{\eta\}_{\text{crit}})) = 0$, whereas $\text{Re}(\lambda_2(\mathbf{k}; \{\eta\}_{\text{crit}})) < 0$. In this case *the bifurcating activity patterns are static*. They were analyzed in [6, 24].
- (2) $\Delta(\mathbf{k}; \{\eta\}_{\text{crit}}) = 0$: $\lambda_1(\mathbf{k}; \{\eta\}_{\text{crit}}) = \lambda_2(\mathbf{k}; \{\eta\}_{\text{crit}})$, this means that two real eigenvalues (of the wave vector $\mathbf{k}$) cross the imaginary axis. This is not a generic case because a large number of parameters has to be chosen appropriately so that $\Delta(\mathbf{k}; \{\eta\}_{\text{crit}})$ vanishes.
- (3) $\Delta(\mathbf{k}; \{\eta\}_{\text{crit}}) < 0$: A complex pair of eigenvalues (of the wave vector $\mathbf{k}$) crosses the imaginary axis: $\lambda_{1,2}(\mathbf{k}; \{\eta\}_{\text{crit}}) = \pm i\omega$, where

$$\omega = \sqrt{-\Delta(\mathbf{k}; \{\eta\}_{\text{crit}})}. \quad (14)$$

From this equation we have the important (necessary) *condition for an oscillatory instability*,

$$\Delta(\mathbf{k}; \{\eta\}_{\text{crit}}) < 0 \quad (15)$$

which has to be fulfilled, otherwise there will not be a complex pair of eigenvalues crossing the imaginary axis. Condition (15) finds a clear physiological interpretation: Taking into account Equation (12) we see that the mutual interactions of activator and inhibitor have to be strong enough in comparison to the self-interactions of activator and inhibitor.

In the present study we investigate the dynamics of the bifurcating activity patterns which are caused by an oscillatory instability. For this reason we assume that Condition (15) is fulfilled.

With the results of the analysis of the symmetry properties of w_{EE} , w_{EI} , w_{IE} , and w_{II} presented in [24] we are able to determine how many complex pairs of eigenvalues become unstable when $\{\eta\} = \{\eta\}_{\text{crit}}$. Due to Equation (10) the wave vectors

$$\begin{aligned} \mathbf{k}_1 &= \begin{pmatrix} k_1 \\ k_2 \end{pmatrix}, & \mathbf{k}_2 &= \begin{pmatrix} k_2 \\ -k_1 \end{pmatrix}, \\ \mathbf{k}_3 &= \begin{pmatrix} -k_1 \\ -k_2 \end{pmatrix}, & \mathbf{k}_4 &= \begin{pmatrix} -k_2 \\ k_1 \end{pmatrix}, \\ \mathbf{k}_5 &= \begin{pmatrix} k_2 \\ k_1 \end{pmatrix}, & \mathbf{k}_6 &= \begin{pmatrix} k_1 \\ -k_2 \end{pmatrix}, \end{aligned} \quad (16)$$

$$\mathbf{k}_7 = \begin{pmatrix} -k_2 \\ -k_1 \end{pmatrix}, \quad \mathbf{k}_8 = \begin{pmatrix} -k_1 \\ k_2 \end{pmatrix}, \quad (17)$$

have identical Fourier modes $\hat{w}_{EE}$, $\hat{w}_{EI}$, $\hat{w}_{IE}$, and $\hat{w}_{II}$ respectively. Consequently these eight Fourier modes have the same pair of eigenvalues which are given by Equation (12):

$$\lambda_{1,2}(\mathbf{k}_1; \eta) = \dots = \lambda_{1,2}(\mathbf{k}_8; \eta). \quad (18)$$

Some or even all of these wave vectors may be identical. For this reason we have to deal with *three types of instability*:

- (i) *A single complex pair of eigenvalues* crosses the imaginary axis iff $\mathbf{k} = (0, 0)$.
- (ii) *Four complex pairs of eigenvalues* cross the imaginary axis iff one of the following conditions is fulfilled:
 - (1) $k_1 = k_2 \neq 0$,
 - (2) $k_1 = -k_2 \neq 0$,
 - (3) Exactly one of the components of $\mathbf{k}_1$ vanishes.
- (iii) *Eight complex pairs of eigenvalues* cross the imaginary axis iff $\mathbf{k}_1 = (k_1, k_2)$ fulfills all three conditions
 - (1) $k_1 \neq k_2$,
 - (2) $k_1 \neq -k_2$,
 - (3) $k_1 \neq 0$ and $k_2 \neq 0$.

4. Disease Mechanisms

Before we discuss different disease mechanisms let us first specify how the control parameter is varied. We assume that one or several of the parameters α_{EE} , α_{EI} , α_{IE} , and α_{II} can be varied. For those parameters which are varied we put

$$\alpha_{XY} = \eta \tilde{\alpha}_{XY}, \quad (19)$$

where X and Y may be E or I . $\tilde{\alpha}_{XY}$ models the sensitivity of the coupling strength α_{XY} to the variation of η which is the control parameter which causes the instability. Let us for instance consider a disease mechanism which is modeled by $\alpha_{EE} = \eta \tilde{\alpha}_{EE}$ and $\alpha_{II} = \eta \tilde{\alpha}_{II}$, where $\tilde{\alpha}_{EE} > \tilde{\alpha}_{II}$. In this case with increasing η , self-excitation as well as self-inhibition of the network increase. The specific feature of this particular disease mechanism is that the self-excitation increases stronger than the self-inhibition. However, if only one parameter is varied it is sufficient to put $\alpha_{XY} = \eta$.

The instability which is caused by the variation of η may be connected with a supercritical as well as a subcritical bifurcation. In both cases we assume that a complex pair of eigenvalues crosses the imaginary axis giving rise to an oscillatory

Figure 1. Subcritical bifurcation (A): $\Gamma(\mathbf{k}_j; \eta)$, i.e. the real part of the eigenvalue of the unstable mode(s) is positive for $\eta < \eta_{\text{crit}} = 4$. Supercritical bifurcation (B): $\Gamma(\mathbf{k}_j; \eta)$ is positive for $\eta > \eta_{\text{crit}} = 4$ (cf. Equation 13). Note that this plot is a schematic illustration, and $\eta_{\text{crit}} = 4$ was chosen arbitrarily.

instability. As a consequence of this we assume that the model parameters are chosen appropriately so that

$$\Delta(\mathbf{k}; \eta_{\text{crit}}) < 0 \quad (20)$$

holds (cf. Condition 15).

4.1 SUPERCRITICAL BIFURCATION

Let $\mathbf{k}_j$ denote the wave vector of a Fourier mode which undergoes a supercritical bifurcation. Furthermore let η_{crit} denote the critical control parameter which is connected with a vanishing real part of the eigenvalue: $\Gamma(\mathbf{k}_j; \eta_{\text{crit}}) = 0$ (cf. Equation 13). In the case of a supercritical bifurcation η is increased so that $\Gamma(\mathbf{k}_j; \eta)$ becomes positive when $\eta > \eta_{\text{crit}}$ (cf. Figure 1) [cf. 8], i.e.

$$\frac{\partial \Gamma(\mathbf{k}_j; \eta_{\text{crit}})}{\partial \eta} > 0, \quad (21)$$

holds. Eight different disease mechanisms may lead to a supercritical bifurcation. From Equation (11) we immediately read off that $\alpha_{EE} = \eta \tilde{\alpha}_{EE}$ has to be increased. Additionally the other parameters (α_{EI} , α_{IE} , α_{II}) may also be increased, where the model parameters have to be chosen appropriately so that Condition (20) is fulfilled. On the whole this yields *eight different disease mechanisms connected with a supercritical bifurcation*:

- (1) $\alpha_{EE} = \eta \tilde{\alpha}_{EE}$: The self-excitability of the activator is increased.
- (2) $\alpha_{EE} = \eta \tilde{\alpha}_{EE}$, $\alpha_{EI} = \eta \tilde{\alpha}_{EI}$: The influence of the activator on activator as well as inhibitor is increased.
- (3) $\alpha_{EE} = \eta \tilde{\alpha}_{EE}$, $\alpha_{IE} = \eta \tilde{\alpha}_{IE}$: The influence of activator as well as inhibitor on the activator is increased.

- (4) $\alpha_{EE} = \eta \tilde{\alpha}_{EE}, \alpha_{EI} = \eta \tilde{\alpha}_{EI}, \alpha_{IE} = \eta \tilde{\alpha}_{IE}$: The influence of activator as well as inhibitor on the activator is increased. Additionally the influence of the activator on the inhibitor is increased.
- (5) $\alpha_{EE} = \eta \tilde{\alpha}_{EE}, \alpha_{II} = \eta \tilde{\alpha}_{II}$: The self-interactions of activator as well as inhibitor are increased.
- (6) $\alpha_{EE} = \eta \tilde{\alpha}_{EE}, \alpha_{II} = \eta \tilde{\alpha}_{II}, \alpha_{EI} = \eta \tilde{\alpha}_{EI}$: The influence of the activator on activator as well as inhibitor is increased. Additionally the self-inhibition of the inhibitor is increased.
- (7) $\alpha_{EE} = \eta \tilde{\alpha}_{EE}, \alpha_{II} = \eta \tilde{\alpha}_{II}, \alpha_{IE} = \eta \tilde{\alpha}_{IE}$: The influence of the inhibitor on activator as well as inhibitor is increased. Additionally the self-excitability of the activator is increased.
- (8) $\alpha_{EE} = \eta \tilde{\alpha}_{EE}, \alpha_{II} = \eta \tilde{\alpha}_{II}, \alpha_{IE} = \eta \tilde{\alpha}_{IE}, \alpha_{EI} = \eta \tilde{\alpha}_{EI}$: The mutual interactions as well as the self-interactions of activator and inhibitor are increased.

4.2 SUBCRITICAL BIFURCATION

Let $\mathbf{k}_j$ be the wave vector of a Fourier mode which undergoes a subcritical bifurcation. η_{crit} denotes the critical control parameter which is connected with a vanishing real part of the eigenvalue, so that $\Gamma(\mathbf{k}_j; \eta_{\text{crit}}) = 0$ holds (cf. Equation 13). In the case of a subcritical bifurcation,

$$\frac{\partial \Gamma(\mathbf{k}_j; \eta_{\text{crit}})}{\partial \eta} < 0 \quad (22)$$

holds. This means that η is decreased so that $\Gamma(\mathbf{k}_j; \eta)$ becomes positive when $\eta < \eta_{\text{crit}}$ (cf. Figure 1) [cf. 8]. From Equation (11) we immediately read off that $\alpha_{II} = \eta \tilde{\alpha}_{II}$ has to be decreased. On the whole there may be *four different disease mechanisms connected with a subcritical bifurcation*:

- (1) $\alpha_{II} = \eta \tilde{\alpha}_{II}$: The self-inhibition of the inhibitor is decreased.
- (2) $\alpha_{II} = \eta \tilde{\alpha}_{II}, \alpha_{EI} = \eta \tilde{\alpha}_{EI}$: The influence of activator as well as inhibitor on the inhibitor is decreased.
- (3) $\alpha_{II} = \eta \tilde{\alpha}_{II}, \alpha_{IE} = \eta \tilde{\alpha}_{IE}$: The influence of the inhibitor on activator as well as inhibitor is decreased.
- (4) $\alpha_{II} = \eta \tilde{\alpha}_{II}, \alpha_{EI} = \eta \tilde{\alpha}_{EI}, \alpha_{IE} = \eta \tilde{\alpha}_{IE}$: The influence of the inhibitor on activator as well as inhibitor is decreased. Additionally the influence of the activator on the inhibitor is decreased.

4.3 HALLUCINATION THRESHOLD

Starting at the resting state, given by $E = I = 0$, the control parameter η is increased (decreased) until it reaches the *hallucination threshold* η_{crit} and causes a supercritical (subcritical) bifurcation. From Equation (13) (cf. Equation 11) it follows that η_{crit} can easily be determined by putting $\Gamma(\mathbf{k}_j; \eta_{\text{crit}}) = 0$. According

to Equation (11) only α_{EE} and α_{II} influence the hallucination threshold, whereas α_{EI} and α_{IE} do not influence it.

No matter which specific disease mechanism we consider, the order parameter equation is derived in the same way. For different disease mechanisms the coefficients of the order parameter equation differ slightly. Thus, depending on the disease mechanism there are small frequency and amplitude shifts of the bifurcating stable activity patterns. Likewise the hallucination thresholds are different for the different mechanisms. Anyhow, in order not to overload the article we only present the analysis of the disease mechanism given by

$$\alpha_{EE} = \eta, \quad (23)$$

where η is increased. So, we investigate what happens to the network when the self-excitability is increased. The frequency shifts caused by the other disease mechanisms are listed in Appendix C.

From Equation (11) we immediately derive the hallucination threshold

$$\eta_{\text{crit}} = \frac{2}{S'_E(0)\hat{w}_{EE}(\mathbf{k}_j)} + \frac{S'_I(0)\alpha_{II}\hat{w}_{II}(\mathbf{k}_j)}{S'_E(0)\hat{w}_{EE}(\mathbf{k}_j)}. \quad (24)$$

We introduce the bifurcation parameter ε by putting

$$\eta = \eta_{\text{crit}} + \varepsilon \quad \text{where} \quad |\varepsilon| \ll 1. \quad (25)$$

Inserting Equation (25) into Equation (7) we obtain

$$a(\mathbf{k}) = -1 + \eta_{\text{crit}} S'_E(0)\hat{w}_{EE}(\mathbf{k}) + \gamma(\mathbf{k})\varepsilon, \quad (26)$$

with

$$\gamma(\mathbf{k}) = S'_E(0)\hat{w}_{EE}(\mathbf{k}). \quad (27)$$

Inserting Equations (23) and (24) into Equation (14), we obtain the frequency of the oscillatory instability:

$$\omega = \sqrt{4S'_E(0)S'_I(0)\alpha_{EI}\alpha_{IE}\hat{w}_{EI}(\mathbf{k}_j)\hat{w}_{IE}(\mathbf{k}_j) - 2[1 + S'_I(0)\alpha_{II}\hat{w}_{II}(\mathbf{k}_j)]}. \quad (28)$$

5. Order Parameter Equation

In this section we will determine the order parameter equation for the three types of instability. We briefly sketch the derivation of the order parameter equation. For further details we refer to [9, 10, 15, 20]. For the sake of shortness let us introduce the abbreviations

$$a = a(\mathbf{k}_j), \quad b = b(\mathbf{k}_j), \quad c = c(\mathbf{k}_j), \quad d = d(\mathbf{k}_j), \quad B = B(\mathbf{k}_j), \quad (29)$$

$$\begin{aligned}\hat{w}_{EE} &= \hat{w}_{EE}(\mathbf{k}_j), \quad \hat{w}_{EI} = \hat{w}_{EI}(\mathbf{k}_j), \\ \hat{w}_{IE} &= \hat{w}_{IE}(\mathbf{k}_j), \quad \hat{w}_{II} = \hat{w}_{II}(\mathbf{k}_j),\end{aligned}\tag{30}$$

for $j = 1$ (if only one Fourier mode becomes unstable) or $j = 1, \dots, 4$ (if four modes become unstable) or $j = 1, \dots, 8$ (if eight modes become unstable). Note that $\mathbf{k}_1, \mathbf{k}_2, \dots$ denote the wave vectors of the unstable Fourier modes.

After projection into the respective eigenspace, the eigenvectors of $\mathbf{k}_1, \mathbf{k}_2, \dots$ are identical. For the derivation of the order parameter equation we need the eigenvectors Φ_0, Φ_1 and the adjoint eigenvectors Ψ^0, Ψ^1 satisfying

$$B\Phi_0 = i\omega\Phi_0, \quad \text{where } \Phi_0 = \begin{pmatrix} b \\ -a + i\omega \end{pmatrix}, \tag{31}$$

$$B\Phi_1 = -i\omega\Phi_1, \quad \text{where } \Phi_1 = \Phi_0^* = \begin{pmatrix} b \\ -a - i\omega \end{pmatrix}, \tag{32}$$

$$B^T\Psi^0 = i\omega\Psi^0, \quad \text{where } \Psi^0 = \frac{-1}{2\omega} \begin{pmatrix} c(\omega - ia)/(\omega^2 + a^2) \\ i \end{pmatrix}, \tag{33}$$

$$B^T\Psi^1 = -i\omega\Psi^1, \quad \text{where } \Psi^1 = \Psi^{0*}. \tag{34}$$

Φ_0^* denotes the complex conjugate of Φ_0 . The eigenvectors and the adjoint eigenvectors fulfill the orthonormality relation

$$(\Phi_n, \Psi^m) = \delta_{nm} \quad (n, m = 0, 1) \tag{35}$$

in the subspace belonging to the wave vector $\mathbf{k}_j$.

The eigenvectors enable us to expand the Fourier modes of activator and inhibitor in the $\mathbf{k}_j$ -subspace:

$$\begin{pmatrix} \hat{E}(\mathbf{k}_j, t) \\ \hat{I}(\mathbf{k}_j, t) \end{pmatrix} = \xi_j \Phi_0 + \mu_j \Phi_1, \quad (j = 1, \dots, 8), \tag{36}$$

where ξ_j and μ_j denote the amplitudes of the order parameters.

Next, we carry out a Fourier transformation of the total nonlinear model Equations (1) and (2). The Fourier transformed model may concisely be written as

$$\frac{d}{dt} \begin{pmatrix} \hat{E}(\mathbf{k}, t) \\ \hat{I}(\mathbf{k}, t) \end{pmatrix} = B(\mathbf{k}) \begin{pmatrix} \hat{E}(\mathbf{k}, t) \\ \hat{I}(\mathbf{k}, t) \end{pmatrix} + \mathbf{N}(\{\hat{E}(\mathbf{k}', t)\}, \{\hat{I}(\mathbf{k}', t)\}, \mathbf{k}), \tag{37}$$

for all wave vectors $\mathbf{k} = (k_1, k_2)$, with integer k_1 and k_2 . $\{\hat{E}(\mathbf{k}', t)\}$ and $\{\hat{I}(\mathbf{k}', t)\}$ denote all Fourier components of the activator and the inhibitor. $B(\mathbf{k})$ is the matrix of the linear part of the vector field (cf. Equation 6). $\mathbf{N}(\{\hat{E}(\mathbf{k}', t)\}, \{\hat{I}(\mathbf{k}', t)\}, \mathbf{k})$ is

a shortform for the nonlinear terms of the vector field projected onto the eigenspace corresponding to the wave vector $\mathbf{k}$ (cf. the Fourier transformed linear problem in Equation 5). For the sake of brevity we introduce the shortform

$$\xi_j^\ominus = \xi_m, \text{ where } \mathbf{k}_m = -\mathbf{k}_j. \quad (38)$$

Thus, the symbol $\ominus$ in $\xi_j^\ominus$ denotes the index corresponding to the wave vector which is the negative of $\mathbf{k}_j$. For instance, $\xi_1^\ominus = \xi_3$ (cf. Equation 16). According to Definition (38) the symbol $\ominus$ will also be applied to other variables.

E and I are real functions. For this reason with Equations (32) and (36) we obtain

$$\xi_j^\ominus \Phi_0 + \mu_j^\ominus \Phi_1 = \begin{pmatrix} \hat{E}(-\mathbf{k}_j, t) \\ \hat{I}(-\mathbf{k}_j, t) \end{pmatrix} = \begin{pmatrix} \hat{E}(\mathbf{k}_j, t)^* \\ \hat{I}(\mathbf{k}_j, t)^* \end{pmatrix} = \xi_j^* \Phi_1 + \mu_j^* \Phi_0, \quad (39)$$

where $*$ denotes the complex conjugate. With $\Phi_1 = \Phi_0^*$ (cf. Equation 32) and the orthonormality Relation (35) we get

$$\xi_j^\ominus = \mu_j^* \text{ and } \mu_j^\ominus = \xi_j^*. \quad (40)$$

Next, we insert Expansion (36) into Equation (37). With Equation (40) and the orthonormality Relation (35) we immediately obtain the order parameter equation

$$\dot{\xi}_j = (\varepsilon' + i\tilde{\omega})\xi_j + (\varepsilon' + i\kappa)\xi_j^{\ominus*} + (\mathbf{N}(\{\hat{E}(\mathbf{k}', t), \hat{I}(\mathbf{k}', t), \mathbf{k}_j\}, \Psi^0)), \quad (41)$$

where $(., .)$ denotes the scalar product (cf. Equation 35). In Equation (41) we use the abbreviations

$$\tilde{\omega} = \omega + \kappa, \quad \kappa = \frac{a(\mathbf{k}_j)b(\mathbf{k}_j)c(\mathbf{k}_j)\gamma(\mathbf{k}_j)}{2\omega(\omega^2 + a^2(\mathbf{k}_j))}\varepsilon, \quad (42)$$

$$\varepsilon' = \frac{-b(\mathbf{k}_j)c(\mathbf{k}_j)\gamma(\mathbf{k}_j)}{2(\omega^2 + a^2(\mathbf{k}_j))}\varepsilon. \quad (43)$$

Next we turn to a rotating coordinate system by putting

$$\xi_j(t) = a_j(t) \exp(i\tilde{\omega}t). \quad (44)$$

Inserting Ansatz (44) into Equation (41) and multiplying both sides with $\exp(-i\tilde{\omega}t)$ we obtain equations for $\dot{a}_1, \dots, \dot{a}_N$. This equation can be written in a concise way by means of the vector

$$\mathbf{a}(t) = \begin{pmatrix} a_1(t) \\ \vdots \\ a_N(t) \end{pmatrix}, \quad (45)$$

Figure 2. Small coefficients $\alpha + i\beta$ and $\alpha - i\beta$ of the nonlinear terms of Equation (46): This is illustrated for $\alpha_{IE}\hat{w}_{IE} = \alpha_{EI}\hat{w}_{EI} = 0.05$, $\alpha_{IE}\hat{w}_{II} = 0.02$, and $S_E(x) = S_I(x) = \rho \tanh(x)$. In (A) we plotted ω over ρ . (A) shows that ρ has to be $> \rho_{\text{crit}} \approx 33.3$, otherwise there is no Hopf bifurcation. In (B) we plotted $\omega / |\alpha + i\beta|$ over ρ . (B) clearly shows that $|\alpha + i\beta|$ is small in comparison to ω . This justifies the application of the averaging theorem. ω , α , and β were determined according to Equation (28) and Equations from appendix A.

where $N = 1$ (single-mode instability), 4 (four-modes instability), 8 (eight-modes instability). With this notation the evolution equation of the complex amplitudes may be written in the form

$$\dot{\mathbf{a}} = \mathbf{f}(\mathbf{a}, T). \quad (46)$$

$\mathbf{f}(\mathbf{a}, T)$ is a periodic vector field because of the terms containing $\exp(i2\tilde{\omega}t)$, $\exp(-i2\tilde{\omega}t)$, and $\exp(-i4\tilde{\omega}t)$. For this reason the period of the vector field is given by $T = \pi/\tilde{\omega}$.

Now let us profit from the fact that within a wide parameter range the dynamics of the $\xi_j(t)$ given by Equation (41) acts on two different time scales: There is a fast oscillation given by $\exp(i\tilde{\omega}t)$. On the other hand the complex amplitudes $a_j(t)$ act on a slow time scale. This can easily be seen by considering the coefficients of Equation (46). ε' and $\varepsilon' + 1\kappa'$, the coefficients of the linear terms, are small because ε is small in the neighbourhood of the bifurcation. On the other hand $\alpha + i\beta$ and $\alpha - i\beta$, the coefficients of the nonlinear terms, are small within a wide parameter range. This is shown in Figure 2.

The fast variables cause a ‘tremor’ of the slow amplitudes which can be extracted by means of the *averaging theorem* (cf. Thm 4.1.1 in [8], Thm 3.2 in [13], Ch. 4 in [1]). The latter enables us to approximate the dynamics of Equation (46) by means of the autonomous system given by

$$\dot{\mathbf{A}}(t) = \mathbf{F}(\mathbf{A}) = \frac{1}{T} \int_0^T \mathbf{f}(\mathbf{A}, t) dt \quad (47)$$

(Thm 4.1.1 in [8]), where the averaged variables are denoted by

$$\mathbf{A}(t) = \begin{pmatrix} A_1(t) \\ \vdots \\ A_N(t) \end{pmatrix} \quad (48)$$

(cf. Equation 45). For the time being we introduce a smallness parameter μ , where $0 \ll \mu < 1$. μ corresponds to the order of magnitude of the coupling coefficients (cf. Figure 2), so that $|\alpha + i\beta| = O(\mu)$. According to the averaging theorem the solution $\mathbf{A}(t)$ of the averaged equation approximates the solution $\mathbf{a}(t)$ of the non-autonomous Equation (46): If $\|\mathbf{a}(0) - \mathbf{A}(0)\| = O(\mu)$ then $\|\mathbf{a}(t) - \mathbf{A}(t)\| = O(\mu)$ on a time scale $t \sim 1/\mu$ (Thm 4.1.1 in [8]). According to Hale, $\mathbf{A}(t)$ approximates $\mathbf{a}(t)$ even for $t \in [0, \infty)$ (Thm 3.2 in [13]).

As a result of the averaging procedure terms containing $\exp(i2\tilde{\omega}t)$, $\exp(-i2\tilde{\omega}t)$, and $\exp(-i4\tilde{\omega}t)$ cancel out, and we are left with the evolution equation of the averaged system:

$$\dot{A}_j = \varepsilon' A_j + [(\mathbf{N}(\{\hat{E}(\mathbf{k}', t)\}, \{\hat{I}(\mathbf{k}', t)\}, \mathbf{k}_j), \Psi^0)]_{\text{av}}. \quad (49)$$

$[\dots]_{\text{av}}$ denotes the nonlinear terms of Equation (41) averaged according to Equation (47). Equation (49) for the single mode instability and for the four-modes as well as eight-modes instability will be presented below.

5.1 SINGLE-MODE INSTABILITY

We first study what happens if only one Fourier mode becomes unstable (cf. Section 3.1). Omitting terms of fourth and higher order we obtain the averaged order parameter equation (cf. Equation 49)

$$\dot{A}_1 = \varepsilon' A_1 - (\alpha + i\beta) A_1 |A_1|^2, \quad (50)$$

where the coefficients are listed in Appendix A. $A_1(t)$ is a complex amplitude. We derive evolution equations for the real amplitude $R(t)$ and the (real) phase $\phi(t)$ by inserting

$$A_1(t) = R(t) \exp[i(\phi(t))] \quad (51)$$

into Equation (49). We obtain evolution equations for amplitude

$$\dot{R} = \varepsilon' R - \alpha R^3, \quad (52)$$

and phase

$$\dot{\phi} = -\beta R^2. \quad (53)$$

$R^{\text{stat}} = 0$ is the stable fixed point if $\varepsilon' < 0$, whereas for $\varepsilon' > 0$ there are two stable states given by

$$R^{\text{stat}} = \pm \sqrt{\frac{\varepsilon'}{\alpha}} \quad \text{and} \quad \phi^{\text{stat}}(t) = -\frac{\beta\varepsilon'}{\alpha}t + \phi^{\text{stat}}(0). \quad (54)$$

According to Equations (36), (38), (40), (44) and (51), activator and inhibitor read

$$E(\mathbf{x}, t) = 2bR(t) \cos [\tilde{\omega}t + \phi(t)] + O(|A_1(t)|^3), \quad (55)$$

$$I(\mathbf{x}, t) = 2(a^2 + \omega^2)R(t) \cos [\tilde{\omega}t + \phi(t) + \theta] + O(|A_1(t)|^3), \quad (56)$$

and θ given by Equation (59), where a and b are shortforms introduced in Equations (29) and (7). $O(|A_1(t)|^3)$ denotes terms of third and higher order of $|A_1(t)|$.

The pattern of activator and inhibitor corresponding to the stable fixed point of the averaged order parameter equation is determined by inserting Equation (54) into Equations (55) and (56):

$$E(\mathbf{x}, t) = \pm 2b\sqrt{\frac{\varepsilon'}{\alpha}} \cos \left[\left(\tilde{\omega} - \frac{\beta\varepsilon'}{\alpha} \right) t + \phi^{\text{stat}}(0) \right] + O(|A_1(t)|^3), \quad (57)$$

$$\begin{aligned} I(\mathbf{x}, t) = & \pm 2(a^2 + \omega^2)\sqrt{\frac{\varepsilon'}{\alpha}} \cos \left[\left(\tilde{\omega} - \frac{\beta\varepsilon'}{\alpha} \right) t + \phi^{\text{stat}}(0) + \theta \right] \\ & + O(|A_1(t)|^3), \end{aligned} \quad (58)$$

where θ is given by

$$\cos \theta = -\frac{a}{a^2 + \omega^2}, \quad \sin \theta = \frac{\omega}{a^2 + \omega^2}. \quad (59)$$

From Equations (57) and (58) we immediately read off that both, activator as well as inhibitor, perform a spatially homogenous oscillation with a constant frequency. Between activator and inhibitor there is a *frequency dependent phase shift* given by θ (cf. Equation 59) and the signs of a and b (cf. Equations 29 and 7).

5.2 FOUR-MODES INSTABILITY

In this section we analyze what happens if four Fourier modes become unstable (cf. Section 3.1). With a little calculation we obtain the averaged order parameter equations:

$$\dot{A}_1 = \varepsilon' A_1 - (\alpha + i\beta) \left\{ A_1 \sum_{k=1}^4 (2 - \delta_{1k}) |A_k|^2 + 2A_3^* A_2 A_4 \right\}, \quad (60)$$

$$\dot{A}_2 = \varepsilon' A_2 - (\alpha + i\beta) \left\{ A_2 \sum_{k=1}^4 (2 - \delta_{2k}) |A_k|^2 + 2A_4^* A_1 A_3 \right\}, \quad (61)$$

$$\dot{A}_3 = \varepsilon' A_3 - (\alpha + i\beta) \left\{ A_3 \sum_{k=1}^4 (2 - \delta_{3k}) |A_k|^2 + 2A_1^* A_2 A_4 \right\}, \quad (62)$$

$$\dot{A}_4 = \varepsilon' A_4 - (\alpha + i\beta) \left\{ A_4 \sum_{k=1}^4 (2 - \delta_{4k}) |A_k|^2 + 2A_2^* A_1 A_3 \right\}, \quad (63)$$

with α and β from Equations (113) and (114) and ε' from Equation (43). Let us check whether the averaged order parameter dynamics is governed by a potential $V(A_1, \dots, A_4, A_1^*, \dots, A_4^*)$, where

$$\dot{A}_j = -\frac{\partial V}{\partial A_j^*} \quad (64)$$

holds [cf. 9, 10]. If a potential V exists the condition

$$\frac{\partial \dot{A}_k}{\partial A_j} = \frac{\partial \dot{A}_j^*}{\partial A_k^*} \quad (65)$$

has to be fulfilled. With a little calculation we immediately see that this condition is not fulfilled for $\beta \neq 0$, whereas for $\beta = 0$ we obtain

$$\begin{aligned} V(A_1, \dots, A_4, A_1^*, \dots, A_4^*) = & -\varepsilon' \sum_{j=1}^4 A_j A_j^* + \frac{\alpha}{2} \sum_{j=1}^4 A_j^2 (A_j^*)^2 \\ & + 2\alpha \sum_{\substack{j,l=1 \\ j < l}}^4 A_j A_j^* A_l A_l^* + \alpha \sum_{j=1}^4 A_j A_j^{\ominus*} A_{k(j)}^{\ominus} A_{k(j)}^{\ominus}. \end{aligned} \quad (66)$$

Next we analyze the stationary solutions of the order parameters. To this end we turn to a rotating coordinate system by means of the Ansatz

$$A_j(t) = R_j(t) \exp[i\phi_j(t)] = R_j(t) \exp[i(\Omega_j t + \varphi_j(t))], \quad (67)$$

where R_j , $\phi(t)$, Ω_j , and φ_j are real. Ω_j and φ_j are used for the analytical investigation, whereas the $\phi_j(t)$ are used for the presentation of the simulations. According to Section 5 A_j is a slowly varying complex amplitude. For this reason $|\Omega_j|$ has to be small, and $\varphi_j(t)$ is a slowly varying phase. Note that Ω_j is a small frequency shift which may differ for all $j = 1, \dots, 4$. Inserting Ansatz (67) into Equation (60) up to (63) we obtain equations for the amplitudes:

$$\dot{R}_1 = \varepsilon' R_1 - \alpha R_1 \sum_{k=1}^4 (2 - \delta_{1k}) R_k^2 - 2R_2 R_3 R_4 (\alpha \cos \Lambda - \beta \sin \Lambda), \quad (68)$$

$$\dot{R}_2 = \varepsilon' R_2 - \alpha R_2 \sum_{k=1}^4 (2 - \delta_{2k}) R_k^2 - 2R_1 R_3 R_4 (\alpha \cos \Lambda + \beta \sin \Lambda), \quad (69)$$

$$\dot{R}_3 = \varepsilon' R_3 - \alpha R_3 \sum_{k=1}^4 (2 - \delta_{3k}) R_k^2 - 2R_1 R_2 R_4 (\alpha \cos \Lambda - \beta \sin \Lambda), \quad (70)$$

$$\dot{R}_4 = \varepsilon' R_4 - \alpha R_4 \sum_{k=1}^4 (2 - \delta_{4k}) R_k^2 - 2R_1 R_2 R_3 (\alpha \cos \Lambda + \beta \sin \Lambda), \quad (71)$$

and for the phases

$$R_1(\Omega_1 + \dot{\varphi}_1) = -\beta R_1 \sum_{k=1}^4 (2 - \delta_{1k}) R_k^2 - 2R_1 R_2 R_3 (\beta \cos \Lambda - \alpha \sin \Lambda), \quad (72)$$

$$R_2(\Omega_2 + \dot{\varphi}_2) = -\beta R_2 \sum_{k=1}^4 (2 - \delta_{2k}) R_k^2 - 2R_1 R_3 R_4 (\beta \cos \Lambda + \alpha \sin \Lambda), \quad (73)$$

$$R_3(\Omega_3 + \dot{\varphi}_3) = -\beta R_3 \sum_{k=1}^4 (2 - \delta_{3k}) R_k^2 - 2R_1 R_2 R_4 (\beta \cos \Lambda - \alpha \sin \Lambda), \quad (74)$$

$$R_4(\Omega_4 + \dot{\varphi}_4) = -\beta R_4 \sum_{k=1}^4 (2 - \delta_{4k}) R_k^2 - 2R_1 R_2 R_3 (\beta \cos \Lambda + \alpha \sin \Lambda), \quad (75)$$

where

$$\Lambda = (\Omega_2 + \Omega_4 - \Omega_1 - \Omega_3)t + \varphi_2 + \varphi_4 - \varphi_1 - \varphi_3. \quad (76)$$

For $\varepsilon' < 0$ the resting state, given by $R_1 = \dots = R_4 = 0$, is stable. For $\varepsilon' > 0$ with a little calculation we get the fixed points of Equations (68) up to (71) and (72) up to (75) obeying

$$\dot{R}_j^{\text{stat}} = 0 \quad \text{and} \quad \dot{\varphi}_j^{\text{stat}} = 0, \quad (77)$$

where R_j^{stat} denotes the amplitude of the fixed point, whereas φ_j^{stat} denotes the phase of the fixed point. In order to check whether these fixed points are stable we have to carry out a linear stability analysis. To this end we put

$$R_j(t) = R_j^{\text{stat}} + \xi_j(t) \quad \text{and} \quad \varphi_j(t) = \varphi_j^{\text{stat}} + \psi_j(t). \quad (78)$$

For the sake of brevity in this section we only mention the stable fixed points, the unstable fixed points are listed in Appendix B.1. There are two different types of fixed points:

(1) *Only one mode survives*: In this case we obtain

$$R_j^{\text{stat}} = \sqrt{\varepsilon'/\alpha} \quad \text{and} \quad R_k^{\text{stat}} = 0 \quad \text{for} \quad k \neq j, \quad (79)$$

$$\Omega_j^{\text{stat}} = -\beta\varepsilon'/\alpha \quad \text{and} \quad \Omega_k^{\text{stat}} = 2\Omega_j^{\text{stat}} \quad \text{for} \quad k \neq j, \quad (80)$$

where Ω_k^{stat} is determined for $R_k \searrow 0$, i.e. for small and positive R_k . For vanishing R_k the corresponding phase of the k th mode is obviously not defined. In order to analyze the linear stability of the fixed point we insert Equations (79) and (80) and Ansatz (78) into Equations (68) up to (71) and (72) up to (75). For the sake of brevity we skip the straightforward calculations and simply give the result. The eigenvalues of the linear problem are: $\lambda_1 = -2\varepsilon'$, $\lambda_2 = \lambda_3 = \lambda_4 = -\varepsilon'$, and $\lambda_5 = 0$. Obviously, the first four eigenvalues are negative and real. The vanishing fifth eigenvalue is due to the SO(2)-symmetry which results from the fact that φ_j^{stat} can be chosen arbitrarily. Note that the linear problem has only five dimensions, because as a consequence of $R_k^{\text{stat}} = 0$ the phases φ_k ($k \neq j$) are not defined.

We have to analyze the spectrum of the linear problem so that we can determine whether the fixed point is stable or unstable. It is well-known that a fixed point is stable if the real parts of all eigenvalues are negative [cf. e.g., 9]. The problem of whether a fixed point is still stable though one of his eigenvalues vanishes is quite sophisticated. Let us recall that the bifurcating solutions of the order parameter equation, the so-called reduced problem, act within the center manifold [see, e.g., 8]. If the linear stability analysis of a fixed point within the center manifold reveals eigenvalues with negative real part and one vanishing eigenvalue, then the fixed point is stable, despite the nonlinear terms. This was rigorously proven by Sattinger [21]. This kind of stability is called *orbital stability* [3]. For the fixed point under consideration this means that the phase φ_j^{stat} of the surviving mode can be shifted arbitrarily, nevertheless the corresponding fixed point will remain stable. As a consequence of the orbital stability noise causes the onset of a dynamical phenomenon which in laser physics is called *phase diffusion* [9]: φ_j^{stat} undergoes noise induced diffusion.

(2) *All modes coexist*, where

$$R_j^{\text{stat}} = \sqrt{\frac{\varepsilon'}{5\alpha}} \quad \text{and} \quad \Omega_j^{\text{stat}} = -\beta\varepsilon'/\alpha \quad \text{for} \quad j = 1, \dots, 4 \quad (81)$$

and

$$\varphi_2^{\text{stat}} + \varphi_4^{\text{stat}} - \varphi_1^{\text{stat}} - \varphi_3^{\text{stat}} = \pi. \quad (82)$$

Figure 3. *Basins of attraction*: Final values of amplitude of mode 1 (A), 2 (B), 3 (C), 4 (D) are plotted for different initial values $R_1(0)$ (ordinate) and $\varphi_1(0)$ (abscissa). Initial conditions determine whether all modes coexist (gray area in (A), (B), (C) and white area in (D)) or whether only one mode survives (mode 1: white area in (A), mode 2: white area in (B), mode 3: white area in (C)).

We inserted Equations (81) and (82) and Ansatz (78) into Equations (68) up to (71) and (72) up to (75) in order to analyze the linear stability of the fixed point. It was not possible to determine the eigenvalues analytically. For this reason we calculated the eigenvalues numerically for a wide range of parameters. According to our numerical investigation the real parts of all except for three eigenvalues were negative. According to Equation (82) three phases can be chosen deliberately giving rise to a threefold $SO(2)$ -symmetry. As a consequence of this, three eigenvalues vanish. Pego and Weinstein proved rigorously that in the case of two vanishing eigenvalues (all others having negative real part) the fixed point is stable irrespective of the nonlinear terms [19]. According to our knowledge up to now there is no rigorous proof for the stability in the case of three vanishing eigenvalues (all others having negative real part). Nevertheless one may expect that the approach presented by Sattinger [21] and Pego and Weinstein [19] may be extended to the case of three vanishing eigenvalues which we are interested in. However, in the present study we preferred a numerical investigation which clearly shows that for a wide range of parameters and initial conditions we observe only the two types of stable fixed points mentioned above.

At this point it becomes obvious that the dynamics determined by Equations (68) up to (71) and (72) up to (75) is *no winner-takes-all dynamics*. The latter is well-known in physics for instance from the Bénard problem [10] and from the synergetic computer [11]. Moreover the author [24] showed that a different disease mechanism as the one analyzed in this study causes a winner-takes-all dynamics in the model of Ermentrout and Cowan [6]. Let us briefly mention the basic feature of

the winner-takes-all dynamics [cf. 10, 11, 24]: Only one mode survives the modes' competition. In several systems which are governed by a winner-takes-all dynamics the mode with the largest (real) initial amplitude wins the competition [cf. 10, 11, 24].

According to our numerical investigation the dynamics given by Equations (68) up to (71) and (72) up to (75) is different:

- (1) Depending on the initial conditions only one or all modes survive.
- (2) If all modes survive they all have the same real amplitude, and the phases obey Equation (82).
- (3) A single surviving mode need not have the largest (real) initial amplitude.

These features are illustrated in Figure 3: We integrated Equations (60) up to (63) for different initial values of $R_1(0)$ and $\varphi_1(0)$ (cf. Equation (67)) and fixed initial values for the other modes, where $R_2(0) = 0.2$, $R_3(0) = 0.18$, $R_4(0) = 0.16$, $\varphi_2(0) = \varphi_3(0) = \varphi_4(0) = 0$. The final values of the mode amplitudes $R_1, \dots, R_4$ are plotted (number of time steps = 6000, stepsize = 0.005).

According to Equations (36), (38), (40), (44), and (67) activator and inhibitor may be written in the form

$$E(\mathbf{x}, t) = 2b \sum_{j=1}^4 R_j(t) \cos [(\tilde{\omega} + \Omega_j)t + \varphi_j(t) + \mathbf{k}_j \cdot \mathbf{x}] + O(\|\mathbf{A}(t)\|^3), \quad (83)$$

$$I(\mathbf{x}, t) = 2(a^2 + \omega^2) \sum_{j=1}^4 R_j(t) \cos [(\tilde{\omega} + \Omega_j)t + \varphi_j(t) + \theta + \mathbf{k}_j \cdot \mathbf{x}] + O(\|\mathbf{A}(t)\|^3), \quad (84)$$

where θ is given by Equation (59). $O(\|\mathbf{A}(t)\|^3)$ denotes terms of third and higher order of $\|\mathbf{A}(t)\|$ with $\mathbf{A}$ according to Equation (48). Note that a and b are shortforms introduced in Equations (29) and (7).

In order to determine the pattern of activator and inhibitor which correspond to the stable fixed points of the averaged order parameter equation we have to insert the equations for amplitudes, phases and frequency shifts into Equations (83) and (84).

(1) *Only one mode survives*: Let j be the index of the mode which wins the modes' competition. Inserting Equations (79) and (80) into Equations (83) and (84), we immediately obtain the stable stationary state generated by the single surviving mode:

$$E(\mathbf{x}, t) = 2b \sqrt{\frac{\varepsilon'}{\alpha}} \cos \left[\left(\tilde{\omega} - \frac{\beta \varepsilon'}{\alpha} \right) t + \varphi_j^{\text{stat}} + \mathbf{k}_j \cdot \mathbf{x} \right] + O(\|\mathbf{A}(t)\|^3), \quad (85)$$

$$\begin{aligned}
I(\mathbf{x}, t) = & 2(a^2 + \omega^2) \sqrt{\frac{\varepsilon'}{\alpha}} \cos \left[\left(\tilde{\omega} - \frac{\beta \varepsilon'}{\alpha} \right) t + \varphi_j^{\text{stat}} + \theta + \mathbf{k}_j \cdot \mathbf{x} \right] \\
& + O(\|\mathbf{A}(t)\|^3).
\end{aligned} \tag{86}$$

Obviously the activity patterns of activator and inhibitor are *travelling waves*, both having the same velocity but different amplitudes. Note that between activator and inhibitor there is a *frequency dependent spatial shift* given by θ (cf. Equations 59) and the signs of a and b (cf. Equations 29 and 7).

(2) *All modes coexist*: Inserting Equations (81) and (82) into Equations (83) and (84), with a little calculation we obtain the stable stationary state evolving in the case of stable coexistence:

$$E(\mathbf{x}, t) = C_1(t) S_1(\mathbf{x}) + C_2(t) S_2(\mathbf{x}) + O(\|\mathbf{A}(t)\|^3), \tag{87}$$

$$I(\mathbf{x}, t) = C_1'(t) S_1(\mathbf{x}) + C_2'(t) S_2(\mathbf{x}) + O(\|\mathbf{A}(t)\|^3), \tag{88}$$

where we used the abbreviations

$$\begin{aligned}
C_1(t) &= C_E \cos \left[\left(\tilde{\omega} - \frac{\beta \varepsilon'}{\alpha} \right) t \right], \\
C_1'(t) &= C_I \cos \left[\left(\tilde{\omega} - \frac{\beta \varepsilon'}{\alpha} \right) t + \theta \right],
\end{aligned} \tag{89}$$

$$\begin{aligned}
C_2(t) &= C_E \cos \left[\left(\tilde{\omega} - \frac{\beta \varepsilon'}{\alpha} \right) t + \frac{\pi}{2} \right], \\
C_2'(t) &= C_I \cos \left[\left(\tilde{\omega} - \frac{\beta \varepsilon'}{\alpha} \right) t + \frac{\pi}{2} + \theta \right],
\end{aligned} \tag{90}$$

$$C_E = 4b \sqrt{\frac{\varepsilon'}{5\alpha}}, \quad C_I = 4(a^2 + \omega^2) \sqrt{\frac{\varepsilon'}{5\alpha}}, \tag{91}$$

$$\begin{aligned}
S_1(\mathbf{x}) &= \cos(\mathbf{k}_1 \cdot \mathbf{x} + \varphi_1^{\text{stat}}), \\
S_2(\mathbf{x}) &= \cos\left(\mathbf{k}_2 \cdot \mathbf{x} + \varphi_2^{\text{stat}} - \frac{\pi}{2}\right).
\end{aligned} \tag{92}$$

The pattern of both, activator as well as inhibitor, consists of two standing waves denoted by $S_1(\mathbf{x})$ and $S_2(\mathbf{x})$. The first standing wave is generated by the Fourier modes with wave vectors $\mathbf{k}_1$ and $\mathbf{k}_3$: both plane waves are propagating in opposite directions. Likewise the plane waves corresponding to the wave vectors $\mathbf{k}_2$ and $\mathbf{k}_4$ move in opposite directions giving rise to the standing wave $S_2(\mathbf{x})$. $\mathbf{k}_1$ and $\mathbf{k}_2$ are perpendicular to each other. Therefore the standing waves $S_1(\mathbf{x})$ and $S_2(\mathbf{x})$ are

perpendicular to each other. Let us first consider the activator. A_1 and A_2 are the amplitudes of the standing waves which are oscillating with a constant frequency $\tilde{\omega} - \beta\varepsilon'/\alpha$, with $\tilde{\omega}$ from Equation (42). Comparing C_1 and C_2 we immediately see that there is a phase shift of $\pi/2$ between both standing waves. For this reason the amplitude of one standing wave vanishes when the amplitude of the other standing wave has its maximum/minimum. Thus, the activator's pattern consists of two successively 'blinking' standing waves which are perpendicular to each other.

Now let us turn to the inhibitor. C'_1 and C'_2 are the amplitudes of the standing waves which are oscillating with a constant frequency $\tilde{\omega} - \beta\varepsilon'/\alpha$, with $\tilde{\omega}$ from Equation (42). Between $C'_1(t)$ and $C'_2(t)$ there is a phase shift of $\pi/2$. Thus, also the pattern of the inhibitor consists of two successively 'blinking' standing waves perpendicular to each other. Comparing the amplitudes of the activator (C_1 and C_2) with the amplitudes of the inhibitor (C'_1 and C'_2), it turns out that there is a *temporal shift* between the dynamics of activator and inhibitor which is due to θ and the sign of b (cf. Equation 91).

The successively 'blinking' standing waves may be called *blinking rolls* in order to emphasize the main difference from the so-called 'blinking state' which is well-known from the convection of binary mixtures [7]. Bestehorn et al. showed that the blinking state is generated by two travelling waves with oscillating (blinking) amplitudes [2]. In contrast to the blinking state the blinking rolls consist of two standing waves with blinking amplitudes.

5.3 EIGHT-MODES INSTABILITY

In this section we analyze what happens if eight Fourier modes become unstable (cf. Section 3.1). With a little calculation we obtain the averaged order parameter equation:

$$\dot{A}_j = \varepsilon' A_j - (\alpha + i\beta) \left\{ A_j \sum_{k=1}^8 (2 - \delta_{jk}) |A_k|^2 + 2A_j^{\ominus*} \sum_{k(j)} A_k A_k^{\ominus} \right\}, \quad (93)$$

with α and β from Equations (113) and (114), ε' from Equation (43), and $j = 1, \dots, 8$. In order to introduce the summation shortform $\sum_{k(j)} A_k A_k^{\ominus}$ used in Equation (93) we recall that there are 4 different pairs of wave vectors (cf. Equations 16 and 17) given by the relationship $(\mathbf{k}_j, \mathbf{k}_j^{\ominus})$ (cf. Equation 38). So, the pairs of wave vectors are $(\mathbf{k}_1, \mathbf{k}_3)$, $(\mathbf{k}_2, \mathbf{k}_4)$, $(\mathbf{k}_5, \mathbf{k}_7)$, $(\mathbf{k}_6, \mathbf{k}_8)$. Likewise we can form 4 different pairs of mode amplitudes corresponding to the wave vectors:

$$(A_1, A_3), (A_2, A_4), (A_5, A_7), (A_6, A_8). \quad (94)$$

$\sum_{k(j)} A_k A_k^{\ominus}$ denotes the summation over all pairs of amplitudes $(A_k, A_k^{\ominus})$ which do not include A_j . For instance, we get

$$\sum_{k(1)} A_k A_k^{\ominus} = A_2 A_4 + A_5 A_7 + A_6 A_8. \quad (95)$$

Inserting Ansatz (67) into Equation (93) we obtain

$$\begin{aligned} \dot{R}_j &= \varepsilon' R_j - \alpha R_j \sum_{k=1}^8 (2 - \delta_{jk}) R_k^2 - 2R_j^\ominus \\ &\quad \times \sum_{k(j)} R_k R_k^\ominus [\alpha \cos \Lambda_{jk}(t) - \beta \sin \Lambda_{jk}(t)], \end{aligned} \quad (96)$$

$$\begin{aligned} R_j(\Omega_j + \dot{\varphi}_j) &= -\beta R_j \sum_{k=1}^8 (2 - \delta_{jk}) R_k^2 \\ &\quad - 2R_j^\ominus \sum_{k(j)} R_k R_k^\ominus [\alpha \sin \Lambda_{jk}(t) + \beta \cos \Lambda_{jk}(t)], \end{aligned} \quad (97)$$

where

$$\Lambda_{jk}(t) = (\Omega_k + \Omega_k^\ominus - \Omega_j - \Omega_j^\ominus)t + \varphi_k + \varphi_k^\ominus - \varphi_j - \varphi_j^\ominus. \quad (98)$$

As for the four-modes instability, the averaged order parameter equation has a potential only if β vanishes. In this case the potential $V(A_1, \dots, A_8, A_1^*, \dots, A_8^*)$ reads

$$\begin{aligned} V(A_1, \dots, A_8, A_1^*, \dots, A_8^*) &= -\varepsilon' \sum_{j=1}^8 A_j A_j^* + \frac{\alpha}{2} \sum_{j=1}^8 A_j^2 (A_j^*)^2 \\ &\quad + 2\alpha \sum_{\substack{j,l=1 \\ j < l}}^8 A_j A_j^* A_l A_l^* + \alpha \sum_{j=1}^4 A_j A_j^{\ominus*} \sum_{k(j)} A_k A_k^\ominus, \end{aligned} \quad (99)$$

where V obeys

$$\dot{A}_j = -\frac{\partial V}{\partial A_j^*}. \quad (100)$$

The resting state, which is given by $R_1 = \dots = R_8 = 0$, is stable for $\varepsilon' < 0$. For $\varepsilon' > 0$, some straightforward calculations provide us with the fixed points of Equations (96) and (97). Thus we have to take into account Condition (77). By analogy with the four-modes instability we perform a linear stability analysis. To this end we insert Ansatz (78) into Equations (96) and (97). In this section we only mention the stable fixed points. The unstable fixed points are summarized in Appendix B.2.

Basically we obtain the same two types of fixed points as in the case of the four-modes instability:

(1) *Only one mode survives*: As in Section 5.2 the fixed point's amplitudes and frequency shifts are given by

$$R_j^{\text{stat}} = \sqrt{\varepsilon'/\alpha} \quad \text{and} \quad R_k^{\text{stat}} = 0 \quad \text{for} \quad k \neq j \quad (101)$$

$$\Omega_j^{\text{stat}} = -\beta\varepsilon'/\alpha \quad \text{and} \quad \Omega_k^{\text{stat}} = 2\Omega_j^{\text{stat}} \quad \text{for} \quad k \neq j, \quad (102)$$

where Ω_k^{stat} is determined for $R_k \searrow 0$ (cf. Equations 79 and 80). The linear stability of the fixed point reveals one vanishing eigenvalue, whereas the real parts of all other eigenvalues are negative (cf. Section 5.2). According to Sattinger [21] this causes *orbital stability* of the fixed point. Thus, noise will give rise to *phase diffusion*.

(2) *Four coexisting modes*: There are two different possibilities concerning the wave vectors of the unstable modes. The four modes consist of two pairs which are of the form $(\mathbf{k}_j, -\mathbf{k}_j)$ and $(\mathbf{k}_l, -\mathbf{k}_l)$. Now there are two possibilities: $\mathbf{k}_j$ may or may not be perpendicular to $\mathbf{k}_l$. This feature does not influence the linear stability but the resulting activity patterns and corresponding hallucinations differ decisively.

(2.1) *Perpendicular pairs*: Let $j = 1$ and $l = 2$ (cf. Equations 16 and 17). The fixed point of the order parameter equation reads:

$$R_j^{\text{stat}} = \sqrt{\frac{\varepsilon'}{5\alpha}} \quad \text{and} \quad \Omega_j^{\text{stat}} = -\beta\varepsilon'/\alpha \quad \text{for} \quad j = 1, \dots, 4, \quad (103)$$

$$R_k^{\text{stat}} = 0 \quad \text{and} \quad \Omega_k^{\text{stat}} = 8\Omega_1^{\text{stat}}/5 \quad \text{for} \quad k = 5, \dots, 8, \quad (104)$$

where Ω_k^{stat} is determined for $R_k \searrow 0$. The phases obey

$$\varphi_2^{\text{stat}} + \varphi_4^{\text{stat}} - \varphi_1^{\text{stat}} - \varphi_3^{\text{stat}} = \pi. \quad (105)$$

(2.2) *Non-perpendicular pairs*: For instance $j = 1$ and $l = 5$ (cf. Equations 16 and 17). In this case we obtain

$$R_j^{\text{stat}} = \sqrt{\frac{\varepsilon'}{5\alpha}} \quad \text{and} \quad \Omega_j^{\text{stat}} = -\beta\varepsilon'/\alpha \quad \text{for} \quad j = 1, 3, 5, 7, \quad (106)$$

$$R_k^{\text{stat}} = 0 \quad \text{and} \quad \Omega_k^{\text{stat}} = 8\Omega_1^{\text{stat}}/5 \quad \text{for} \quad k = 2, 4, 6, 8, \quad (107)$$

where Ω_k^{stat} is determined for $R_k \searrow 0$. The phases obey

$$\varphi_5^{\text{stat}} + \varphi_7^{\text{stat}} - \varphi_1^{\text{stat}} - \varphi_3^{\text{stat}} = \pi. \quad (108)$$

Note that for a given standing wave there are always two different non-perpendicular pairs. For instance, if the first standing wave is formed by the modes with wave vectors $\mathbf{k}_1$ and $\mathbf{k}_3$, a non-perpendicular standing wave may be formed by the modes with wave vectors $\mathbf{k}_5$ and $\mathbf{k}_7$ as well as those with wave vectors $\mathbf{k}_6$ and $\mathbf{k}_8$. Both cases are connected with qualitatively different visual hallucinations. This will be discussed below.

In order to investigate the linear stability of these two types of fixed points we have to insert Ansatz (78) and Equations (103) up to (105) or (106) up to (108) into Equations (96) and (97). The analysis of the linear stability of the fixed point with perpendicular pairs as well as the fixed point with the non-perpendicular pairs reveals the same results: As in Section 5.2 in the case of the coexistence of four modes we determined the eigenvalues numerically for a wide range of parameters because it was not possible to calculate the eigenvalues analytically. Three eigenvalues vanish, whereas all others have negative real part. As a result of Equations (105) and (108) there is a threefold $SO(2)$ -symmetry. For the same reason as in Section 5.2 one may expect that an extension of the approach of Sattinger [21] and Pego and Weinstein [19] may provide us with a rigorous proof of the stability of the fixed points under consideration.

Anyhow, we carried out a numerical investigation which clearly shows that for a wide range of parameters and initial conditions there are only three different types of stable fixed points corresponding to: (1) a single surviving mode, (2) four coexisting modes with perpendicular pairs of wave vectors, (3) four coexisting modes with non-perpendicular pairs of wave vectors. In particular the coexistence of all eight modes is not stable.

Our numerical analysis shows that the dynamics of the eight-modes instability governed by Equations (96) and (97) is *no winner-takes-all dynamics*. Rather it exhibits the following features which are similar to those of the four-modes instability analyzed in Section 5.2:

- (1) Depending on the initial conditions only one or four modes survive.
- (2) If four modes survive they all have the same real amplitude, and the phases obey Equation (105) or (108).
- (3) The four coexisting modes may have perpendicular or non-perpendicular pairs of wave vectors.
- (4) A single surviving mode need not have the largest (real) initial amplitude.

In order to determine the bifurcating activity patterns in lowest order we expand activator and inhibitor in terms of the order parameters according to Equations (36), (38), (40), (44), and (67) so that we obtain

$$\begin{aligned}
 E(\mathbf{x}, t) = & 2b \sum_{j=1}^8 R_j(t) \cos [(\tilde{\omega} + \Omega_j)t + \varphi_j(t) + \mathbf{k}_j \cdot \mathbf{x}] \\
 & + O(\|\mathbf{A}(t)\|^3),
 \end{aligned} \tag{109}$$

$$\begin{aligned}
I(\mathbf{x}, t) = & 2(a^2 + \omega^2) \sum_{j=1}^4 R_j(t) \cos[(\tilde{\omega} + \Omega_j)t + \varphi_j(t) \\
& + \theta + \mathbf{k}_j \cdot \mathbf{x}] + O(\|\mathbf{A}(t)\|^3),
\end{aligned} \tag{110}$$

where θ is given by Equation (59). Terms of third and higher order of $\|\mathbf{A}(t)\|$ are denoted by $O(\|\mathbf{A}(t)\|^3)$, where $\mathbf{A}$ is introduced in Equation (48).

In order to determine the bifurcating stable patterns of activator and inhibitor corresponding to the stable fixed points of the averaged order parameter equation we have to insert the Equations for amplitudes, phases and frequency shifts into Equations (109) and (110).

(1) *Only one mode survives*: We derive the stable stationary state generated by the single surviving mode by inserting Equations (101) and (102) into Equations (109) and (110). Immediately we obtain Equations (85) and (86), where j is the index of the mode which wins the modes' competition.

In Section 5.2 we discussed the activity pattern given by Equations (85) and (86) in detail. Activator and inhibitor are *travelling waves* with the same velocity but different amplitudes. Between activator and inhibitor there is a *frequency dependent shift* given by θ (cf. Equation 59) and the signs of a and b (cf. Equations 29 and 7).

(2) *Four modes coexist*: Inserting Equations (103) up to (105) or (106) up to (108) into Equations (109) and (110), with a little calculation we obtain the stable bifurcating pattern in the case of stable coexistence of four modes (cf. Equations 87 and 88):

$$E(\mathbf{x}, t) = C_1(t) S_1(\mathbf{x}) + C_2(t) S_2(\mathbf{x}) + \text{h.o.t.}, \tag{111}$$

$$I(\mathbf{x}, t) = C_1'(t) S_1(\mathbf{x}) + C_2'(t) S_2(\mathbf{x}) + \text{h.o.t.}, \tag{112}$$

with amplitudes $C_j(t)$, $C_j(t)'$ and standing waves $S_j(\mathbf{x})$ from Equations (89) up to (92). The pattern given by Equations (111) and (112) was discussed in detail in Section 5.2: activator as well as inhibitor generate *blinking rolls*. In the case of two *perpendicular pairs* of wave vectors of the unstable modes the rolls, i.e. the two standing waves denoted by $S_1(\mathbf{x})$ and $S_2(\mathbf{x})$ are perpendicular to each other. On the other hand if there are two *non-perpendicular pairs* of wave vectors the rolls $S_1(\mathbf{x})$ and $S_2(\mathbf{x})$ are not perpendicular to each other.

6. Numerical Simulation

In this section the averaged order parameter equations of the four-modes instability and the eight-modes instability are integrated numerically. In order to derive the hallucination patterns from the pattern of the cortical activity we have to take into account the *visuo-cortical transformation* [4, cf. 5]. Sufficiently far away from the fovea this transformation corresponds to the complex logarithm [4, 22], so that a

point on the retina with the complex coordinate z is mapped onto a point of the cortex with the complex coordinate $\ln(z)$.

In order to illustrate the variety of emerging hallucinations we integrate the stationary solutions of the averaged order parameter equations for different unstable wave vectors.

Several physiological parameters [cf. 6] which correspond to the mutual neuronal interactions determine the shapes of w_{EE} , w_{EI} , w_{IE} , and w_{II} . According to our analysis of the linear problem these parameters determine which Fourier modes become unstable. On a large time scale the neuronal interactions may undergo variations, those, for instance, caused by circadian rhythms. For this reason the shapes of w_{EE} , w_{EI} , w_{IE} , and w_{II} vary on this large time scale, too. Thus, at different times on the long time scale as a consequence of the variation of the control parameter η different Fourier modes will undergo one of the instabilities analyzed in this study. For instance, at one time a four-modes instability occurs, whereas at a different time an eight-modes instability occurs. Obviously the ‘hallucination threshold’ η_{crit} given by Equation (24) varies on this large time scale, too.

According to Equations (57) and (58), in the case of the single-mode instability a spatially homogenous blinking occurs. Complex dynamical hallucinations are caused by the four-modes as well as the eight-modes instability.

6.1 FOUR-MODES INSTABILITY

According to the results presented in Section 5.2 one or four modes may survive giving rise to travelling waves or blinking rolls.

6.1.1 Travelling waves

Figure 4 shows the dynamics of the averaged order parameter Equation (60) up to (63) in a case where only mode survives. In Figure 5 we plotted the corresponding frequency shifts. In order to investigate the emerging stable cortical activity pattern we plotted the activator according to Equation (85). Obviously $\mathbf{k}_j = (k_{j1}, k_{j2})$, the wave vector of the travelling wave given by Equation (85) crucially determines the type of the visual hallucination. According to the visuo-cortical transformation [4] three different hallucinations are connected with a travelling wave of cortical activity:

- (1) *Rotating spirals*: The wave vector of the surviving mode, determines the shape of the spiral. That means $\mathbf{k}_j$ determines the number of arms of the spiral and its elicity (right-handed versus left-handed) (cf. Figure 6). Moreover the spiral rotates with frequency $\tilde{\omega} - \beta\varepsilon'/\alpha$ (cf. Equation 85). The sign of $\mathbf{k}_j$ determines whether the rotation is right-handed or left-handed.
- (2) *Tunnel hallucination*: One of the components of the wave vector vanishes. In this case the hallucination consists of concentric rings with increasing or decreasing radius (cf. Figure 7). The sign of the non-vanishing component

Figure 4. *Four-modes instability*: Amplitudes $R_j(t)$ (solid lines) and real parts $\text{Re}(A_j(t))$ (dotted lines) are plotted over time ($j = 1, \dots, 4$). Mode 2 wins the modes' competition (although $R_1(0) > R_2(0)$). Parameters and initial conditions: $\alpha = \beta = \varepsilon = 1$, $R_1(0) = 0.21$, $R_2(0) = 0.2$, $R_3(0) = 0.18$, $R_4(0) = 0.16$, $\phi_1(0) = 0.5$, $\phi_2(0) = \phi_3(0) = \phi_4(0) = 0$ (cf. Figure 3). Amplitudes in the stationary state totally agree with the analytical results given by Equation (79).

Figure 5. *Four-modes instability*: Frequency shifts $\dot{\phi}_j(t)$ are plotted over time ($j = 1, \dots, 4$) (cf. Equation 67). Same simulation as in Figure 4. Frequency shifts in the stationary state totally agree with the analytical results given by Equation (80).

of the wave vector determines whether the radiuses increase or decrease. For this reason the sign of the wave vector determines whether the hallucination corresponds to *moving forward or backward through a tunnel*.

Figure 6. Spiral hallucinations: The coordinates of the visual hallucination are $x = r \cos \theta$ (abscissa) and $y = r \sin \theta$ (ordinate) ((B) and (D)). According to the visuo-cortical transformation [4] the cortical coordinates are $\log r$ (ordinate) and θ (abscissa). The hallucinations in (B) and (D) correspond to the cortical activity patterns in (A) ($\mathbf{k}_j = \pm(6, 6)$) and (C) ($\mathbf{k}_j = (\pm 6, \mp 6)$). In all activity and hallucination plots white areas correspond to maximal values, whereas black areas correspond to minimal values.

Figure 7. Tunnel and funnel hallucinations: Coordinates as in Figure 6. The hallucinations in (B) and (D) correspond to the cortical activity patterns in (A) ($\mathbf{k}_j = (\pm 6, 0)$) and (C) ($\mathbf{k}_j = (0, \mp 6)$).

Figure 8. *Four-modes instability*: Amplitudes $R_j(t)$ (solid lines) and real parts $\text{Re}(A_j(t))$ (dotted lines) are plotted over time ($j = 1, \dots, 4$). All modes coexist (although $R_1(0) > R_2(0)$). Parameters and initial conditions: $\alpha = \beta = \varepsilon = 1$, $R_1(0) = 0.21$, $R_2(0) = 0.2$, $R_3(0) = 0.18$, $R_4(0) = 0.16$, $\phi_1(0) = 2$, $\phi_2(0) = \phi_3(0) = \phi_4(0) = 0$ (cf. Figure 3). Amplitudes in the stationary state totally agree with the analytical results given by Equation (81).

- (3) *Rotating funnel*: If the other component of the wave vector vanishes a star (funnel) rotates with constant rotation velocity $\tilde{\omega} - \beta\varepsilon'/\alpha$ (cf. Equation 85, Figure 7). The sign of the wave vector $\mathbf{k}_j$ determines whether the rotation is right-handed or left-handed. Moreover the number of arms of the star is given by $\mathbf{k}_j$ (cf. Figure 7).

6.1.2 Blinking rolls

Figure 8 shows the dynamics of the averaged order parameter Equation (60) up to (63) with parameters and initial conditions giving rise to four coexisting modes. In Figure 9 we plotted the corresponding frequency shifts and phase difference. The emerging cortical activity pattern and the corresponding dynamical hallucination decisively depends on the wave vectors of the coexisting modes (cf. Equation 87). According to the visuo-cortical transformation [4] two different dynamical hallucinations emerge:

- (1) *Blinking spirals*: Figure 10 shows the cortical activity which is generated by two blinking standing waves perpendicular to each other. Consequently the visual hallucination consists of oscillatory transitions between a spiral with right-handed elicity and a spiral with left-handed elicity, both having the same number of arms (cf. Figure 11).

Figure 9. *Four-modes instability*: Frequency shifts $\dot{\phi}_j(t)$, phase difference $\Lambda(t)$ (solid line), and π (dotted line) are plotted over time ($j = 1, \dots, 4$) (cf. Equations 67 and 76). Same simulation as in Figure 4. Frequency shifts and phase difference in the stationary state totally agree with the analytical results given by Equations (81) and (82).

Figure 10. *Blinking rolls of the four-modes instability*: The cortical activity pattern given by Equation (87) is plotted at different times for $\mathbf{k}_1 = (2, 2)$. Time proceeds through one period T row by row from the left upper corner to the right lower corner in equidistant steps $T/16$, where $T = 2\pi/(\bar{\omega} - \beta\varepsilon'/\alpha)$ is the period of the oscillation according to Equation (85).

- (2) *Blinking tunnels and funnels*: Figure 12 shows two blinking standing waves of cortical activity giving rise to oscillatory transitions between a tunnel and a funnel hallucination as shown in Figure 13.

Figure 11. *Blinking spirals*: Hallucination patterns corresponding to cortical activity patterns of Figure 10. The plots are arranged as in Figure 10.

Figure 12. *Blinking rolls of the four-modes instability*: The cortical activity pattern given by Equation (87) is plotted at different times for $\mathbf{k}_1 = (6, 0)$. Time proceeds through one period T row by row from the left upper corner to the right lower corner in equidistant steps $T/16$, where $T = 2\pi/(\tilde{\omega} - \beta\varepsilon'/\alpha)$ is the period of the oscillation according to Equations (87), (89), and (90).

6.2 EIGHT-MODES INSTABILITY

In Section 5.3 we showed that one or four modes may survive the eight modes' competition. The dynamics of the order parameters causes travelling waves or blinking rolls of cortical activity.

Figure 13. *Blinking tunnels (rings) and funnels (stars)*: Hallucination patterns corresponding to cortical activity patterns of Figure 12. The plots are arranged as in Figure 12.

Figure 14. *Eight-modes instability*: Amplitudes $R_j(t)$ (solid lines) and real parts $\text{Re}(A_j(t))$ (dotted lines) are plotted over time ($j = 1, \dots, 4$). Mode 1 wins the modes' competition. Modes 5, $\dots$, 8 are plotted in Figure 15. Parameters and initial conditions: $\alpha = \beta = \varepsilon = 1$, $R_1(0) = 0.2$, $R_2(0) = 0.19$, $R_3(0) = 0.18$, $R_4(0) = 0.17$, $\phi_1(0) = \dots, \phi_4(0) = 0$ (cf. Figure 3). Amplitudes in the stationary state totally agree with the analytical results given by Equation (101).

6.2.1 Travelling waves

Figures 14 and 15 show how a single mode wins the competition of eight modes determined by the averaged order parameter Equation (93). In Figures 16 and 17 the corresponding frequency shifts are plotted. In order to illustrate the emerging stable

Figure 15. *Eight-modes instability*: Amplitudes $R_j(t)$ (solid lines) and real parts $\text{Re}(A_j(t))$ (dotted lines) are plotted over time ($j = 5, \dots, 8$). Mode 1 wins the modes' competition. Modes 1, $\dots$, 4 are plotted in Figure 14. Parameters and initial conditions: $\alpha = \beta = \varepsilon = 1$, $R_5(0) = 0.16$, $R_6(0) = 0.15$, $R_7(0) = 0.14$, $R_8(0) = 0.13$, $\phi_5(0) = \dots, \phi_8(0) = 0$ (cf. Figure 3). Amplitudes in the stationary state totally agree with the analytical results given by Equation (101).

Figure 16. *Eight-modes instability*: Frequency shifts $\dot{\phi}_1(t), \dots, \dot{\phi}_4(t)$ are plotted over time (cf. Equation 67). Same simulation as in Figure 14. Frequency shifts in the stationary state totally agree with the analytical results given by Equation (102).

cortical activity pattern we plotted the activator according to Equation (85). Obviously $\mathbf{k}_j = (k_{j1}, k_{j2})$, the wave vector of the travelling wave given by Equation (85) crucially determines the type of the visual hallucination. As a consequence of the visuo-cortical transformation [4], a travelling wave is connected with hallucinated *rotating spirals*. The wave vector of the surviving mode determines the shape

Figure 17. *Eight-modes instability*: Frequency shifts $\dot{\phi}_j(t)$ are plotted over time ($j = 5, \dots, 8$) (cf. Equation 67). Same simulation as in Figure 15. Frequency shifts in the stationary state totally agree with the analytical results given by Equation (102).

Figure 18. *Spiral hallucinations*: The hallucinations in (B) and (D) correspond to the cortical activity patterns in (A) ($\mathbf{k}_j = \pm(2, 3)$) and (B) ($\mathbf{k}_j = (\mp 2, \pm 3)$). Coordinates as in Figure 6.

of the spiral (number of arms and elicity) (cf. Figure 18). The spiral rotates with frequency $\tilde{\omega} - \beta\epsilon'/\alpha$ (cf. Equation 85), where the sign of $\mathbf{k}_j$ determines whether this rotation is right-handed or left-handed.

Figure 19. *Eight-modes instability*: Amplitudes $R_j(t)$ (solid lines) and real parts $\text{Re}(A_j(t))$ (dotted lines) are plotted over time ($j = 1, \dots, 4$). The four modes coexist. Modes 5, $\dots$, 8 are plotted in Figure 20. Parameters and initial conditions: $\alpha = \beta = \varepsilon = 1$, $R_1(0) = 0.2$, $R_2(0) = 0.19$, $R_3(0) = 0.18$, $R_4(0) = 0.17$, $\phi_1(0) = \pi$, $\phi_2(0), \dots, \phi_4(0) = 0$. Amplitudes in the stationary state totally agree with the analytical results given by Equation (103).

6.2.2 Blinking rolls

Figures 19 and 20 show the dynamics of the averaged order parameter, Equation (93), where four modes coexist. Corresponding frequency shifts and phase difference are plotted in Figures 21 and 22. The emerging cortical activity pattern as well as the corresponding dynamical hallucination crucially depend on the wave vectors of the coexisting modes. According to the visuo-cortical transformation [4] three different blinking spiral hallucinations occur:

- (1) The spirals have different number of arms and different elicity (Figures 23 and 24).
- (2) The spirals have different number of arms but the same elicity (Figures 25 and 26).
- (3) The spirals have the same number of arms but different elicity (Figures 27 and 28).

7. Discussion

We analyzed the dynamics of the well-known activator–inhibitor model of Ermentrout and Cowan [6]. Varying control parameters in this model, for instance, increasing the excitability of the network, causes spontaneous pattern formation [cf. 6, 24].

Our results show that the dynamics of the emerging activity crucially depends on whether the mutual interactions between activator and inhibitor are stronger or weaker than the self-interactions of activator and inhibitor. According to

Figure 20. *Eight-modes instability*: Amplitudes $R_j(t)$ (solid lines) and real parts $\text{Re}(A_j(t))$ (dotted lines) are plotted over time ($j = 5, \dots, 8$). Modes 1, $\dots$, 4 are plotted in Figure 19. Parameters and initial conditions: $\alpha = \beta = \varepsilon = 1$, $R_5(0) = 0.16$, $R_6(0) = 0.15$, $R_7(0) = 0.14$, $R_8(0) = 0.13$, $\phi_5(0) = \dots, \phi_8(0) = 0$ (cf. Figure 3). Amplitudes in the stationary state totally agree with the analytical results given by Equation (104).

Figure 21. *Eight-modes instability*: Frequency shifts $\dot{\phi}_1(t), \dots, \dot{\phi}_4(t)$, phase difference $\Lambda_{12}(t)$ (solid line), and π (dotted line) are plotted over time (cf. Equations 67 and 98). Same simulation as in Figure 19. Frequency shifts in the stationary state totally agree with the analytical results given by Equation (103) and (105).

Condition (15) stronger mutual interactions between activator and inhibitor are connected with an oscillatory instability, whereas weaker mutual interactions are connected with a non-oscillatory instability.

Non-oscillatory instabilities were analytically analyzed for different disease mechanisms by Ermentrout and Cowan [6] and by the author [24]. The corre-

Figure 22. *Eight-modes instability*: Frequency shifts $\dot{\phi}_j(t)$ are plotted over time ($j = 5, \dots, 8$) (cf. Equation 67). Same simulation as in Figure 15. Frequency shifts in the stationary state totally agree with the analytical results given by Equation (104).

Figure 23. *Blinking rolls of the eight-modes instability*: The cortical activity pattern given by Equation (111) is plotted at different times, where $\mathbf{k}_1 = (4, 2)$, $\mathbf{k}_3 = -\mathbf{k}_1$, $\mathbf{k}_2 = (2, -4)$, and $\mathbf{k}_4 = -\mathbf{k}_2$ are the wave vectors of the unstable modes. Time proceeds through one period T row by row from the left upper corner to the right lower corner in equidistant steps $T/16$, where $T = 2\pi/(\bar{\omega} - \beta\varepsilon'/\alpha)$ is the period of the oscillation according to Equations (111), (89), and (90).

sponding bifurcating activity patterns are *static spatial patterns* like plane waves and hexagonal patterns [6, 24]. According to the visuo-cortical transformation [4, cf. 5] such kind of brain activity leads to *static visual hallucinations*: static spiral,

Figure 24. *Blinking spirals*: Hallucination patterns corresponding to cortical activity patterns of Figure 23. The plots show oscillatory transitions between spirals with two arms and right-handed elicity and spirals with four arms and left-handed elicity. The plots are arranged as in Figure 23.

Figure 25. *Blinking rolls of the eight-modes instability*: The cortical activity pattern given by Equation (111) is plotted at different times, where $\mathbf{k}_1 = (4, 2)$, $\mathbf{k}_3 = -\mathbf{k}_1$, $\mathbf{k}_5 = (2, 4)$, and $\mathbf{k}_7 = -\mathbf{k}_5$ are the wave vectors of the unstable modes. The plots are arranged as in Figure 23.

tunnel, and funnel hallucinations [6, 24] well-known from clinical observation [16, 23].

An *oscillatory instability* of the model of Ermentrout and Cowan [6] is analytically analyzed for the first time in this article. Let us sketch our results:

Figure 26. *Blinking spirals*: Hallucination patterns corresponding to cortical activity patterns of Figure 25. The plots show oscillatory transitions between spirals with two arms and spirals with four arms, both having right-handed elicity. The plots are arranged as in Figure 23.

Figure 27. *Blinking rolls of the eight-modes instability*: The cortical activity pattern given by Equation (111) is plotted at different times, where $\mathbf{k}_1 = (4, 2)$, $\mathbf{k}_3 = -\mathbf{k}_1$, $\mathbf{k}_6 = (4, -2)$, and $\mathbf{k}_8 = -\mathbf{k}_6$ are the wave vectors of the unstable modes. The plots are arranged as in Figure 23.

(1) A huge variety of different disease mechanisms may cause an oscillatory instability provided the mutual interactions between activator and inhibitor are strong enough in comparison to the self-interactions of activator and inhibitor, i.e. Condition (15) has to be fulfilled.

(2) According to the disease mechanism under consideration a control parameter is varied, for instance, the excitability of the network is increased. The variation of

Figure 28. *Blinking spirals*: Hallucination patterns corresponding to cortical activity patterns of Figure 25. The plots show oscillatory transition between spirals with right-handed elicity and spirals with left-handed elicity, both having two arms. The plots are arranged as in Figure 23.

the control parameter causes a bifurcation. The emerging stable activity patterns are *dynamical spatio-temporal patterns*, e.g. *travelling waves* and *blinking rolls*, i.e. standing waves oscillating with the same frequency and with a phase shift of $\pi/2$.

In order to show this we explicitly derived the order parameter equation. The averaging theorem (cf. Thm 4.1.1 in [8], Thm 3.2 in [13], Ch. 4 in [1]) enabled us to derive the averaged order parameter equation which we analyzed analytically. The model's parameters determine whether a single-mode, a four-modes or an eight-modes instability occurs. In all cases we determined the averaged order parameter equation. In the case of the four-modes as well as the eight-modes instability the averaged order parameter equation has a potential only under conditions which from the physiological point of view cannot be considered to be generic ($\beta = 0$). Depending on model parameters and on initial conditions there are two possible outcomes of the four modes' as well as the eight modes' competition: Only one mode wins or four modes coexist.

Our approach enables us to simulate the dynamics of the model in the neighbourhood of the instability by simply integrating the averaged order parameter equation. This is a big advantage in comparison to tedious integrations of the model equation itself (cf. the simulations in [17]).

(3) Explicitly calculating the stable bifurcating activity patterns in lowest order enabled us to investigate the corresponding visual hallucinations in detail. The emerging activity patterns correspond to *dynamical visual hallucinations*. For different disease mechanisms the amplitudes and frequencies of the activity patterns slightly differ. In the case of the single-mode instability a spatially homogenous

blinking occurs, whereas in the case of the four-modes as well as the eight-modes instability a variety of different dynamical hallucinations occur:

Travelling waves of cortical activity correspond to *rotating spirals* or *rotating funnels (stars)* or *dynamical tunnel hallucinations*, i.e. a hallucinated motion backwards or forwards through a tunnel (cf. Figures 6, 7, and 18).

Blinking rolls of cortical activity lead to *oscillatory transitions between tunnels and funnels* or *oscillatory transitions between spirals with different numbers of arms and different elicity* (cf. Figures 10 up to 13 and 23 up to 28).

The wave vectors of the order parameters determine which visual hallucination occurs. Moreover the initial conditions decisively determine whether travelling waves or blinking rolls occur.

The influence of noise on the dynamics of the model of Ermentrout and Cowan (Equations 1 and 2) was discussed in detail by the author [24]. According to Haken [10], additive Gaussian white noise causes fluctuations of the amplitudes as well as the phases of the order parameters. We showed that in particular *phase diffusion* occurs.

According to our results there is a temporal or spatial shift between activator and inhibitor (cf. Equations 57–59, 85–88, 111 and 112). Thus, the question arises whether the hallucination pattern corresponds to activator or inhibitor? Or do interactions of both contribute to the hallucination pattern?

Finally we remark that by displaying the theoretically derived dynamical visual hallucinations as movies on the computer an interesting phenomenon occurs: As soon as the movie is stopped a motion in the opposite direction is perceived for a while. For instance, immediately after stopping the rotation of a spiral or funnel (star) the spiral or funnel is perceived to rotate in the opposite direction although it actually does not rotate any more. Likewise after stopping the hallucinated motion through a tunnel (which e.g. corresponds to increasing radiuses of concentric rings) the motion in the opposite direction is perceived (corresponding to decreasing radiuses of concentric rings). This indicates that the theoretically derived hallucination patterns may be suitable tools for visual stimulation experiments.

Appendix A: Coefficients α and β

The coefficients of the order parameter equation (50) read

$$\alpha = \frac{S'''(0)}{12\omega} \left[\frac{c(a\tilde{d} + \omega\tilde{c})}{\omega^2 + a^2} - \tilde{g} \right], \quad (113)$$

$$\beta = \frac{S'''(0)}{12\omega} \left[\frac{c(\omega\tilde{d} + a\tilde{c})}{\omega^2 + a^2} + \tilde{f} \right], \quad (114)$$

where

$$\begin{aligned}\tilde{c} = & 3\alpha_{EE}^3\hat{w}_{EE}^3b^3 + 9\alpha_{EE}^2\hat{w}_{EE}^2\alpha_{IE}\hat{w}_{IE}ab^2 \\ & + 9\alpha_{EE}\hat{w}_{EE}\alpha_{IE}^2\hat{w}_{IE}^2a^2b + 3\alpha_{IE}^3\hat{w}_{IE}^3a(a^2 + \omega^2) \\ & + 3\alpha_{EE}\hat{w}_{EE}\alpha_{IE}^2\hat{w}_{IE}^2\omega^2b, \end{aligned} \quad (115)$$

$$\begin{aligned}\tilde{d} = & -3\alpha_{EE}^2\hat{w}_{EE}^2\alpha_{IE}\hat{w}_{IE}\omega b^2 - 6\alpha_{EE}\hat{w}_{EE}\alpha_{IE}^2\hat{w}_{IE}^2ab\omega \\ & - 3\alpha_{IE}^3\hat{w}_{IE}^3\omega(\omega^2 + a^2), \end{aligned} \quad (116)$$

$$\begin{aligned}\tilde{f} = & 3\alpha_{EI}^3\hat{w}_{EI}^3b^3 + 9\alpha_{EI}^2\hat{w}_{EI}^2\alpha_{II}\hat{w}_{II}ab^2 + 9\alpha_{EI}\hat{w}_{EI}\alpha_{II}^2\hat{w}_{II}^2a^2b \\ & + 3\alpha_{II}^3\hat{w}_{II}^3a(a^2 + \omega^2) + 3\alpha_{EI}\hat{w}_{EI}\alpha_{II}^2\hat{w}_{II}^2\omega^2b, \end{aligned} \quad (117)$$

$$\begin{aligned}\tilde{g} = & -3\alpha_{EI}^2\hat{w}_{EI}^2\alpha_{II}\hat{w}_{II}\omega b^2 - 6\alpha_{EI}\hat{w}_{EI}\alpha_{II}^2\hat{w}_{II}^2ab\omega \\ & - 3\alpha_{II}^3\hat{w}_{II}^3\omega(\omega^2 + a^2). \end{aligned} \quad (118)$$

For the sake of brevity we used abbreviations (29) and (30).

Appendix B: Unstable Fixed Points

B.1 FOUR-MODES INSTABILITY

In Section 5.2 we analyzed the dynamics of the four-modes instability. In the following we list the unstable fixed points of the dynamics given by Equations (68) up to (71) and (72) up to (75). All of them are saddle points. This can easily be shown by a linear stability analysis based on the Ansatz (78). If $R_k^{\text{stat}} = 0$ the frequency shift Ω_k is determined in the limit $R_k \searrow 0$ (cf. Section 5.2). We summarize the saddle points:

(1) *Two coexisting modes*, where $\mathbf{k}_j$ and $-\mathbf{k}_j$ are the wave vectors of the coexisting modes. Note that this is only possible if $\beta = 0$. Let $j = 1$. The fixed point reads $R_1^{\text{stat}} = R_3^{\text{stat}} = \sqrt{\varepsilon'/(3\alpha)}$, $R_2^{\text{stat}} = R_4^{\text{stat}} = 0$, $\Omega_1^{\text{stat}} = \dots = \Omega_4^{\text{stat}} = 0$, and $\varphi_1 + \varphi_3 = \varphi_2 + \varphi_4$.

(2) *Two coexisting modes*, where $\mathbf{k}_j$ and $\mathbf{k}_l$ are the wave vectors of the coexisting modes, and $\mathbf{k}_j \perp \mathbf{k}_l$ holds. Let $j = 1$. We obtain $R_1^{\text{stat}} = R_3^{\text{stat}} = \sqrt{\varepsilon'/(3\alpha)}$, $R_2^{\text{stat}} = R_4^{\text{stat}} = 0$, $\Omega_1^{\text{stat}} = \Omega_2^{\text{stat}} = -\beta\varepsilon'/\alpha$, $\Omega_3^{\text{stat}} = \Omega_4^{\text{stat}} = -\Omega_1^{\text{stat}}$, and $\varphi_1 + \varphi_3 = \varphi_2 + \varphi_4$.

(3) *Three coexisting modes*, where $\mathbf{k}_j$, $-\mathbf{k}_j$, and $\mathbf{k}_l$ are the wave vectors of the coexisting modes, and $\mathbf{k}_j \perp \mathbf{k}_l$ holds. Let $j = 1$. Note that this fixed point only exists if $\alpha = \beta$. The fixed point reads $R_1^{\text{stat}} = \dots = R_3^{\text{stat}} = \sqrt{\varepsilon'/(6\alpha)}$, $R_4^{\text{stat}} = 0$, $\Omega_1^{\text{stat}} = \dots = \Omega_4^{\text{stat}} = -\beta 5\varepsilon'/(6\alpha)$, and $\cos(\varphi_1 + \varphi_3 - \varphi_2 + \varphi_4) = \sin(\varphi_1 + \varphi_3 - \varphi_2 + \varphi_4)$.

(4) *Four coexisting modes*: The unstable fixed point reads $R_1^{\text{stat}} = \dots = R_4^{\text{stat}} = (\sqrt{\varepsilon'/\alpha})/3$, $\Omega_1^{\text{stat}} = \dots = \Omega_4^{\text{stat}} = -\beta\varepsilon'/\alpha$, and $\varphi_1 + \varphi_3 = \varphi_2 + \varphi_4$.

B.2 EIGHT-MODES INSTABILITY

The dynamics of the eight-modes instability was analyzed in Section 5.3. In this section we summarize the unstable fixed points of the dynamics given by Equations (96) and (97). The linear stability analysis is straightforward. Based on the Ansatz (78) for some unstable fixed points the linear stability analysis can be performed analytically, for some one has to determine the spectrum of the linear problem numerically, and in three cases the stability has to be tested directly numerically. Note that the frequency shift Ω_k is determined in the limit $R_k \searrow 0$ if $R_k^{\text{stat}} = 0$ (cf. Section 5.2). The unstable fixed points read:

(1) *Two coexisting modes*: Suppose the j th and the l th mode survive. In this case we obtain $R_j^{\text{stat}} = R_l^{\text{stat}} = \sqrt{\varepsilon'/(3\alpha)}$, $R_m^{\text{stat}} = 0$, and $\Omega_j^{\text{stat}} = \Omega_k^{\text{stat}} = -\beta\varepsilon'/\alpha$, $\Omega_m^{\text{stat}} = -\beta 4\varepsilon'/(3\alpha)$, where $m \neq j$ and $m \neq l$.

(2) *Three coexisting modes*: Suppose the j th and the l th mode survive. In this case we obtain $R_j^{\text{stat}} = \dots = R_l^{\text{stat}} = \sqrt{\varepsilon'/(3\alpha)}$, $R_m^{\text{stat}} = 0$, $\Omega_j^{\text{stat}} = \Omega_k^{\text{stat}} = -\beta\varepsilon'/\alpha$, and $\Omega_m^{\text{stat}} = -\beta 4\varepsilon'/(3\alpha)$, where $m \neq j$ and $m \neq l$.

(3) *Four coexisting modes*, where $\mathbf{k}_j$, $-\mathbf{k}_j$ and $\mathbf{k}_l$, $-\mathbf{k}_l$ are the wave vectors of the coexisting modes. We get $R_j^{\text{stat}} = R_j^{\text{stat}\ominus} = R_l^{\text{stat}} = R_l^{\text{stat}\ominus} = (\sqrt{\varepsilon'/\alpha})/3$, all other amplitudes vanish. $\Omega_j^{\text{stat}} = \Omega_j^{\text{stat}\ominus} = \Omega_l^{\text{stat}} = \Omega_l^{\text{stat}\ominus} = -\beta\varepsilon'/\alpha$, all other frequency shifts $= -8\beta\varepsilon'/(9\alpha)$, and $\varphi_1 + \varphi_3 = \varphi_2 + \varphi_4$.

(4) *Four coexisting modes*, where the corresponding wave vectors are all perpendicular to each other, for instance: $R_1^{\text{stat}} = R_2^{\text{stat}} = R_5^{\text{stat}} = R_6^{\text{stat}} = \sqrt{\varepsilon'/(7\alpha)}$, all other amplitudes vanish. $\Omega_1^{\text{stat}} = \Omega_2^{\text{stat}} = \Omega_5^{\text{stat}} = \Omega_6^{\text{stat}} = -\beta\varepsilon'/\alpha$, all other frequency shifts $= -8\beta\varepsilon'/(7\alpha)$.

(5) *Five coexisting modes* with two perpendicular pairs of wave vectors: $(\mathbf{k}_j, -\mathbf{k}_j)$ and $(\mathbf{k}_l, -\mathbf{k}_l)$, where $\mathbf{k}_j \perp \mathbf{k}_l$, for instance $j = 1, l = 2$. In this case we get $R_1^{\text{stat}} = \dots = R_4^{\text{stat}} = \sqrt{\varepsilon'/(11\alpha)}$, $R_5^{\text{stat}} = \sqrt{\varepsilon'/(33\alpha)}$, $\Omega_1^{\text{stat}} = \dots = \Omega_4^{\text{stat}} = -15\beta\varepsilon'/(11\alpha)$, $\Omega_5^{\text{stat}} = -\beta\varepsilon'/\alpha$, all other frequency shifts $= -14\beta\varepsilon'/(11\alpha)$, and $\varphi_2 + \varphi_4 - \varphi_1 - \varphi_3 = \pi$.

(6) *Five coexisting modes* with two non-perpendicular pairs of wave vectors: $(\mathbf{k}_j, -\mathbf{k}_j)$ and $(\mathbf{k}_l, -\mathbf{k}_l)$, where $\mathbf{k}_j \perp \mathbf{k}_l$ does not hold, for instance $j = 1, l = 5$. We obtain $R_1^{\text{stat}} = R_3^{\text{stat}} = R_5^{\text{stat}} = R_7^{\text{stat}} = \sqrt{\varepsilon'/(11\alpha)}$, $R_2^{\text{stat}} = \sqrt{\varepsilon'/(33\alpha)}$, $\Omega_1^{\text{stat}} = \Omega_2^{\text{stat}} = \Omega_3^{\text{stat}} = \Omega_5^{\text{stat}} = \Omega_7^{\text{stat}} = -\beta\varepsilon'/\alpha$, $\Omega_6^{\text{stat}} = \Omega_8^{\text{stat}} = -14\beta\varepsilon'/(11\alpha)$, and $\varphi_5 + \varphi_7 - \varphi_1 - \varphi_3 = \pi$.

(7) *Six coexisting modes* with three pairs of wave vectors: $(\mathbf{k}_j, -\mathbf{k}_j)$, $(\mathbf{k}_l, -\mathbf{k}_l)$, and $(\mathbf{k}_m, -\mathbf{k}_m)$, for instance $j = 1, l = 2$, and $m = 5$. We get $R_1^{\text{stat}} = \dots = R_5^{\text{stat}} = R_7^{\text{stat}} = \sqrt{\varepsilon'/(15\alpha)}$, $\Omega_1^{\text{stat}} = \dots = \Omega_5^{\text{stat}} = \Omega_7^{\text{stat}} = -\beta\varepsilon'/\alpha$, $\Omega_6^{\text{stat}} = \Omega_8^{\text{stat}} = -4\beta\varepsilon'/(5\alpha)$, $\Lambda_{jl}(0) = 0$, $\sin \Lambda_{jl}(0) = 0$, $\cos \Lambda_{jl}(0) = 1$, where $j, l = 1, 2, 5$ (cf. Equation 98).

(8) *Six coexisting modes* with two pairs of wave vectors: $(\mathbf{k}_j, -\mathbf{k}_j)$, $(\mathbf{k}_l, -\mathbf{k}_l)$, $\mathbf{k}_m$, and $\mathbf{k}_n$, where $\mathbf{k}_m \perp \mathbf{k}_n$, for instance $j = 1$, $l = 2$, $m = 5$, and $n = 6$. We get $R_1^{\text{stat}} = \dots = R_4^{\text{stat}} = \sqrt{\varepsilon'/(17\alpha)}$, $R_5^{\text{stat}} = R_6^{\text{stat}} = \sqrt{3\varepsilon'/(17\alpha)}$, $\Omega_1^{\text{stat}} = \dots = \Omega_6^{\text{stat}} = -\beta\varepsilon'/\alpha$, $\Omega_7^{\text{stat}} = \Omega_8^{\text{stat}} = -20\beta\varepsilon'/(17\alpha)$, $\varphi_1 + \varphi_3 - \varphi_2 - \varphi_4 = \pi$.

(8) *Eight coexisting modes*: $R_1^{\text{stat}} = \dots = R_8^{\text{stat}} = \sqrt{\varepsilon'/(21\alpha)}$, $\Omega_1^{\text{stat}} = \dots = \Omega_8^{\text{stat}} = -\beta\varepsilon'/\alpha$, $\Lambda_{jl}(0) = 0$, where $j, l = 1, \dots, 8$ (cf. Equation 98).

(9) *Eight coexisting modes*: $R_1^{\text{stat}} = \dots = R_8^{\text{stat}} = \sqrt{\varepsilon'/(13\alpha)}$, $\Omega_1^{\text{stat}} = \dots = \Omega_8^{\text{stat}} = -\beta\varepsilon'/\alpha$. In this case and in case 10 for the sake of brevity we introduce two groups $\{1, 2, 3, 4\}$ and $\{5, 6, 7, 8\}$. $\Lambda_{jk}(0) = \pi$ if j and k are within the same group. Moreover we have to distinguish between two different cases according to $\Lambda_{16} = \Lambda_{25} = 0$ (π), $\Lambda_{15} = \Lambda_{26} = \pi$ (0), $\cos \Lambda_{16} = \cos \Lambda_{25} = 1$ (-1), $\cos \Lambda_{15} = \cos \Lambda_{26} = -1$ (1) (second case in brackets), with Λ_{jk} from Equation (98).

(10) *Eight coexisting modes*: $R_1^{\text{stat}} = \dots = R_8^{\text{stat}} = \sqrt{\varepsilon'/(17\alpha)}$, $\Omega_1^{\text{stat}} = \dots = \Omega_8^{\text{stat}} = -\beta\varepsilon'/\alpha$. $\Lambda_{jk}(0) = 0$ if j and k are within the same group. Moreover we have to distinguish between the two different cases listed in 9.

Appendix C: Frequency Shifts

We briefly sketch the derivation of the frequency shifts connected with the different disease mechanisms summarized in Section 4. For every parameter α_{XY} which is $= \tilde{\alpha}_{XY}\eta$ we expand the corresponding coefficient a , b , c , d in powers of ε . To this end in analogy to Equations (26) and (27) we introduce the abbreviations $\tilde{a}(\mathbf{k}), \dots, \tilde{d}(\mathbf{k})$ and $\gamma_2(\mathbf{k}), \dots, \gamma_4(\mathbf{k})$ with

$$a(\mathbf{k}) = -1 + S'_E(0)\tilde{\alpha}_{EE}\eta_{\text{crit}}\hat{w}_{EE}(\mathbf{k}) = \tilde{a}(\mathbf{k}) + \varepsilon\gamma(\mathbf{k}), \quad (119)$$

$$\begin{aligned} b(\mathbf{k}) &= -S'_E(0)\tilde{\alpha}_{IE}\eta_{\text{crit}}\hat{w}_{IE}(\mathbf{k}) - \varepsilon S'_E(0)\tilde{\alpha}_{IE}\hat{w}_{IE}(\mathbf{k}) \\ &= \tilde{b}(\mathbf{k}) + \varepsilon\gamma_2(\mathbf{k}), \end{aligned} \quad (120)$$

$$\begin{aligned} c(\mathbf{k}) &= S'_I(0)\tilde{\alpha}_{EI}\eta_{\text{crit}}\hat{w}_{EI}(\mathbf{k}) + \varepsilon S'_I(0)\tilde{\alpha}_{EI}\hat{w}_{EI}(\mathbf{k}) \\ &= \tilde{c}(\mathbf{k}) + \varepsilon\gamma_3(\mathbf{k}), \end{aligned} \quad (121)$$

$$\begin{aligned} d(\mathbf{k}) &= -1 - S'_I(0)\tilde{\alpha}_{II}\eta_{\text{crit}}\hat{w}_{II}(\mathbf{k}) - \varepsilon S'_I(0)\tilde{\alpha}_{II}\hat{w}_{II}(\mathbf{k}) \\ &= \tilde{d}(\mathbf{k}) + \varepsilon\gamma_4(\mathbf{k}) \end{aligned} \quad (122)$$

(cf. Equation 8).

The hallucination threshold η_{crit} can easily be calculated according to Section 4.3. With these notations the matrix of the linear problem reads

$$B(\mathbf{k}) = \begin{pmatrix} \tilde{a}(\mathbf{k}) & \tilde{b}(\mathbf{k}) \\ \tilde{c}(\mathbf{k}) & \tilde{d}(\mathbf{k}) \end{pmatrix} + \varepsilon \begin{pmatrix} \gamma(\mathbf{k}) & \gamma_2(\mathbf{k}) \\ \gamma_3(\mathbf{k}) & \gamma_4(\mathbf{k}) \end{pmatrix} \quad (123)$$

(cf. Equation 6). Along the lines of our analysis presented in Section 5 with a little calculation we get the shifted frequency

$$\tilde{\omega} = \omega + \varepsilon \left\{ \frac{abc}{2\omega(\omega^2 + a^2)}\gamma - \frac{c}{2\omega}\gamma_2 + \frac{b}{2\omega}\gamma_3 - \frac{a}{2\omega}\gamma_4 \right\} \quad (124)$$

a , b , c , and ω have to be evaluated for $\eta = \eta_{\text{crit}}$. In particular ω can easily be determined by means of Equation (14).

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