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Decentralised gathering on a discrete field: coupling reaction-diffusion and chemotaxis as social amoebae do

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Abstract

We address the question as to which are the minimal ingredients to obtain a decentralised gathering of agents that move on a lattice according to discrete local rules. The agents and their environment are described with a stochastic model inspired from biology: the aggregation of the *Dictyostelium discoideum* cellular slime mold. The environment transmits information according to a reaction-diffusion mechanism and the agents move by following excitation fronts. We show that despite its simplicity this model exhibits interesting properties of self-organisation. Moreover, first observations show that the system has interesting robustness properties, as being able to resist to the presence of obstacles on the lattice.

keywords:

bio-inspired modelling ; cellular automata ; multi-agent systems ; self-organisation ; aggregation ; reaction-diffusion ; *Dictyostelium discoideum* ; phase transitions

foreword:

The dynamical evolution of the experiments shown in this article can be viewed in form of animations at the address:

<http://www.loria.fr/~fates/Amibes/expe.html>

1 Introduction

1.1 Decentralised Gathering

Let us consider the problem of forming a group by using only local rules. Imagine real or virtual agents that move on a lattice and need to group to form a compact cluster. The agents, all identical, have no idea of their own position, nor do they have on the position of the other agents. All they can do is to send messages that can be relayed, possibly with errors, by the cells of the lattice. The agents have only a rudimentary level of perception and a limited repertoire of actions: they can perceive the state of only the neighbouring cells and the only actions they can undertake is to move to these cells or change the state of these cells.

The main question is to determine what are the minimal ingredients involved to achieve a decentralised gathering with these constraints. More precisely, we wish to know whether we can produce a simple discrete model that will be able to achieve this gathering. By “simple”, we mean using a small number of states for the propagation of messages and a small number of rules for controlling the moves of the agents. In this work, we propose a first step in examining this problem.

This problem can be related to the Leader Election problem [13] where all cells are initially in the same state and where the goal is to attain a configuration in which a single cell is in a distinguished state. In our problem, the objective is to form a cluster with the agents initially dispersed in random locations ; so it can also be seen as a form of symmetry breaking where some special location has to be chosen by consensus. By contrast with diffusion-limited aggregation, where fractal clusters are formed by random walks of particles, we want the clusters to be compact and efficiently generated. The *amorphous computing* paradigm [1], which uses dispersion of the agents and the introduction of noise in the system, also relates to our work. In such a context, solving the decentralised gathering problem may be used to aggregate components, which can constitute a first step before making computations.

1.2 Biological Inspiration

The cellular slime mold *Dictyostelium discoideum* is a fascinating organism that has the ability to live as a mono-cellular organism and to transform into a multi-cellular organism when needed. In normal conditions, the cells live as single individuals by eating decaying logs, humus and bacteria (*e.g.*, [6]). However, when the environment becomes depleted of food, a gathering phenomenon is triggered and single cells aggregate to form a complex organism that will move and react with coordinated changes. The transformation from a group of individual amoebae into a multi-cellular aggregate is a complex phenomenon that involves different stages. In this work, we take inspiration from the first stage of the multi-cellular organisation process, the *aggregation* stage, which consists in gathering all the cells in a compact mass called a *mound* (*e.g.*, [19]).

Observations of *in vitro* experiments show that this aggregation is triggered

by the spontaneous emergence of “pacemakers” or “signalling centres” (*e.g.*, [7]). These pacemakers are formed by one or several cells that attract other cells that are located in their vicinity. Once the first pacemakers are formed, they are in an unstable situation: under normal conditions, they struggle against each other and merge until only a few pacemakers remain ; these will attract other cells to them to form a group where cell differentiations will occur. From a quantitative point of view, the order of magnitude of the size of an amoeba is $10\mu m$, the size of the aggregates can be up to 10^5 individual cells, the gathering can occur on a distance as far as 20 mm [3, 6].

The signalling occurs by transmission of waves, which follow typical evolving reaction-diffusion patterns. The waves are constituted of high-concentration profiles of cyclic adenosine monophosphate (cAMP), an intercellular messenger that serves to guide the moves of the amoebae: this phenomenon is called *chemotaxis* in the biological context and we will use it by analogy to qualify the moves of our virtual agents. The origin of these reaction-diffusion patterns resides in the concomitant realisation of four actions: (a) a cell synthesises cAMP internally until there is enough product to be emitted ; (b) when an amoeba detects a high increase in external cAMP concentration, it follows the concentration gradient (chemotaxis) and releases its own internal cAMP (exocytosis) (c) it then becomes insensitive to cAMP during a given refractory period , (d) in the meanwhile, the cAMP released diffuses and excites other sensitive cells, etc.

Our proposition is to take the essential ingredients of this aggregation mechanism: we examine a model described by simple rules that couple reaction-diffusion and chemotaxis. These laws are parametrised by three probabilities ; we show that for particular setting of these probabilities, the model provides a first solution to the problem of achieving a quick and efficient decentralised gathering.

The next section draws a quick review of modelling reaction-diffusion and chemotaxis. Section 3 describes formally a model that uses reaction-diffusion and chemotaxis to achieve decentralised gathering. In Section 4, we present experiments to explore how the model solves the decentralised gathering problem. To fix the limits of our model, we study the robustness when submitted to various perturbations in Section 5. Finally, we conclude with a short discussion on the coupling of reaction-diffusion and chemotaxis and how it may be possible to use the decentralised gathering of agents in computer science or robotics.

2 Existing models

It is out of scope of this article to give a detailed review of the models that have been proposed to study the dynamics of *Dictyostelium*. We will here simply cite some works as entry points to the literature on the subject, referring to the work of Nagano for a review [18].

Among the first models proposed to model chemotaxis, the proposition of Keller and Segel [14] inspired many works on *Dictyostelium*. Their model used two continuous variables, the chemoattractant’s concentration and the density

of bacteria, which evolve in one dimension according to a simple partial differential equations. To our knowledge, the work of MacKay [15] constitutes one of the first attempts to validate models by comparing simulation outputs with observations of the aggregation stage in *Dictyostelium*. The author explicitly modelled the amoebae as independent agents whose actions are updated according to a centralised time-driven procedure.

The work of Martiel and Goldbeter [17] was an authoritative reference from which numerous other models were derived. It explicitly modelled the state of the cAMP receptors, thus explaining the reaction-diffusion waves of cAMP as a consequence of activation and inhibition of these receptors.

In many works, the aggregation process is triggered by artificially selecting one or several cells as initial pacemakers. The question of knowing whether it is realistic to have a single cell for triggering the whole aggregation process was examined in [7]. The authors showed that this was indeed possible for a particular range of values. However, their model is composed of no less than forty variables or functions and this makes it difficult to understand for the non-specialist.

The techniques of modelling evolved, along with computation power, culminating in impressive simulation results in the years 1990. We refer to the work by Weijer *et al.* (*e.g.*, [20]) or Marée *et al.* (*e.g.*, [16]) to see examples of successful modelling by using partial differential equations.

A major part of the literature is composed of continuous or hybrid models ; to our knowledge, no *fully* discrete model was proposed for capturing *Dictyostelium*'s behaviour. By fully discrete, we mean that time and space are discrete and the state of the cells is described in qualitative terms rather than quantitative (integers or decimal values). Indeed, even when authors propose simplified models (*e.g.*, [3]), the coding of the models often remains complex, thus making the reproduction of the experiments a difficult task.

The reaction-diffusion mechanism alone is well understood and the links between the discrete and continuous models can be explicitly formulated (*e.g.*, [22]). The computational complexity of reaction-diffusion simple model was also examined: Golès and Matamala showed that three states are sufficient for obtaining universality [10] ; Adamatzky studied some problem-solving abilities of reaction-diffusion models [2]. Our work is meant as a further exploration of this field, adding virtual chemotaxis as a new feature to study.

3 A Reaction-diffusion-chemotaxis Model

The reaction-diffusion-chemotaxis model we present belongs to the category of stochastic discrete dynamical systems as time, space and state are discrete. By contrast with other models, it is meant to be as simple as possible, thus providing a tool to examine *sufficient* conditions under which decentralised aggregation is possible. Two layers compose it: the *environmental* layer is a cellular automaton that models a reaction-diffusion process while the *particle* layer describes the moves of virtual amoebae (or simply *amoebae* in the following). The notations

Table 1: Notations used in the description of the model

(p_T, p_E, p_R) transmission rate, emission rate, thermal agitation
$\mathcal{B}, \mathcal{C}, \mathcal{D}, \mathcal{R}$ random operations
$c \in \mathcal{L}$ cell of the grid
σ_c^t State of c at time t
P_c^t Population of c at time t
N_c/E_c^t cells / excited cells in the neighb. of c at time t
$\tilde{N}_c/\tilde{E}_c^t$	free cells / excited free cells in the neighb. of c at time t

we use to present the model are summarised in Table 1.

3.1 The environmental layer

Space is modelled by a regular lattice $\mathcal{L} = \{1, \dots, X\} \times \{1, \dots, Y\}$ in which each cell $c = (c_x, c_y) \in \mathcal{L}$ is associated to a state. The set of possible states for each cell is $\{0, \dots, M\}$, the state of cell c at time t is denoted by σ_c^t .

The state 0 is the *neutral* state, the state M is the *excited* state. A cell may evolve from the neutral state to the excited state if at least one of its neighbours is excited (rule R1). To model the uncertainty on this transition, we will consider that it happens with a given probability p_T , called the *transmission rate*.

The states 1 to $M - 1$ are the *refractory states*. A cell in a refractory state evolves in an autonomous way by decrementing its state by 1 (rule R2) until it reaches the neutral state. A neutral cell surrounded by neutral cells stays neutral (rule R3). We will call neutral, excited, or refractory, a cell of a given configuration that is in the neutral, excited, or refractory state, respectively.

To express these rules without ambiguity, for a cell $c \in \mathcal{L}$, let us denote by N_c the neighbourhood of this cell. Let E_c^t be the set of excited cells in the neighbourhood of c at time t : $E_c^t = \{d \in N_c \mid \sigma_d^t = M\}$. We also denote by $|X|$ the cardinal of a set X .

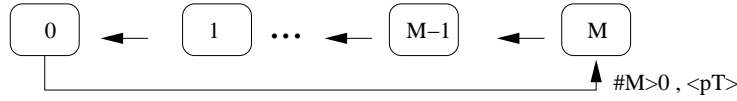


Figure 1: Transition rule of the environmental layer (simple reaction-diffusion)

With these notations, for a time $t \in \mathbb{N}$ and a cell $c \in \mathcal{L}$, let $B(p)$ be a Bernoulli random variable, *i.e.*, a random variable that equals 1 with probability p and equals 0 with probability $1 - p$; the local rule governing the evolution of the environment is:

$$\sigma_c^{t+1} = \begin{cases} M & \text{if } \sigma_c^t = 0 \text{ and } |E_c^t| > 0 \text{ and } \mathcal{B}(p_T) = 1 & (R1) \\ \sigma_c^t - 1 & \text{if } \sigma_c^t \in \{1, \dots, M\} & (R2) \\ 0 & \text{otherwise} & (R3) \end{cases}$$

These rules can be represented in Figure 1.

A set of adjacent cells that are all in the excited state M is called an *excitation front*. In the next paragraph, we explain how the excitation fronts guide the amoebae for moving on the lattice (chemotaxis).

3.2 The particle layer

The amoebae are supposed to be all identical, and in constant number as no birth or death process is considered. We suppose that, contrarily to classical agents, amoebae are *not* autonomous agents: instead they are passive particles that are moved from a cell to a neighbouring cell. As we need to express the moves of amoebae formally, the first point to clarify is how to deal with simultaneous moves of amoebae on the same cell.

There are many policies that can be applied, here we arbitrarily allow only one amoeba to move *from* a non-empty cell at each time step. Note that although this policy appears somehow “natural”, it does not limit the number of amoebae that can simultaneously move *to* a given cell.

How do we deal with this second problem of mutual exclusion of amoebae on a cell? Following [19], we arbitrarily choose to allow an amoeba to go on a neighbouring cell only if this cell contains less than two amoebae. Note that although this rule enables some flexibility on collective moves and suppresses some unwanted discretisation effects, it does not directly limit the number of amoebae that can be located on the same cell.

Let us define a cell that contains no amoeba as an *empty* cell ; a cell that contains less than two amoebae as a *free* cell. The movement rules state that, at each time step, for each non-empty cell, one single amoeba may:

- move to an adjacent free cell randomly chosen (noise rule R4),
- move to an adjacent excited cell (chemotaxis rule R5),
- stay on the same cell (rule R6).

In order to remove ambiguities on the latter formulation, we need to clarify the following questions: How do we apply the noise? How do we select an excited cell if many are visible in the neighbourhood?

To apply the noise rule R4, we will consider that each non-empty cell gives an amoeba to one of its neighbour with probability p_R , called the *agitation rate*. This neighbour is selected at random among all the *free* neighbours. Similarly, to apply the chemotaxis rule R5, amoebae move to a cell randomly selected among the excited free cells of the neighbourhood. However, this mechanism can be refined, for example by assigning smaller weights to diagonal cells in order to overcome discretisation effects.

We can now express these rules formally. For $t \in \mathbb{N}$ and $c \in \mathcal{L}$, let \tilde{N}_c^t , respectively \tilde{E}_c^t , be the set of *free* cells, respectively *excited free* cells, in the neighbourhood of c . For a finite set S , we denote by $\mathcal{R}(S)$ the operation of selecting one element in S with uniform probability. \mathcal{R} will be used to select randomly a neighbour for moving. Let \mathcal{C} be a Bernoulli function. \mathcal{C} will be used to impose noise on the moves of an amoeba with probability p_R .

To represent the move of one amoeba from a non-empty cell c to another cell Δ_c^t , adopting the convention that $\Delta_c^t = \emptyset$ if no move occurs, we have:

$$\text{if } \mathcal{C}(p_R) = 1 \text{ then } \left\{ \begin{array}{ll} \text{if } |\tilde{N}_c^t| > 0 & \text{then } \Delta_c^t = \mathcal{R}[\tilde{N}_c^t] \quad (R4) \\ & \text{else } \Delta_c^t = \emptyset \quad (R6) \end{array} \right.$$

$$\text{else } \left\{ \begin{array}{ll} \text{if } \sigma_c^t = 0 \text{ and } |\tilde{E}_c^t| > 0 & \text{then } \Delta_c^t = \mathcal{R}[\tilde{E}_c^t] \quad (R5) \\ & \text{else } \Delta_c^t = \emptyset \quad (R6) \end{array} \right.$$

For $t \in \mathbb{N}$, let us denote by P_c^t the population of a cell c ; it updates following:

$$P_c^{t+1} = P_c^t + |\{d \in \mathcal{L} \mid \Delta_d^t = c\}| - |\{\Delta_c^t\}|$$

There are other formulations of these rules. For example, we may also express the number of amoebae $\Delta_{c,d}^t$ moving from a non-empty cell c to another cell d at time t asq a function of \tilde{E}_c^t , $\mathcal{R}[\tilde{E}_c^t]$ and $\mathcal{C}(p_R)$. From a programming point of view, what is most important to notice is : (a) our point of view is a cellular-automaton point of view rather than a multi-agent one, *i.e.* actions are cell-centered, amoebae are represented by an attribute of cells rather by an independent list of agents ; (b) the noise rule is the first in priority ; this means that for high values of noise, attraction effects to the excitation fronts are likely to be destroyed by this noise. Weaker versions of noise are possible, for example by moving randomly only if no excitation fronts are visible.

3.3 Coupling of environment and particles

Amoebae act on the environment by emitting excitations that propagate to neighbouring cells. In order to further simplify the model, we deliberately formulate the excitation rule by considering only empty and non-empty cells, without taking into account the number of amoebae contained in each cell. This rule implies that there is no reinforcement in emitting excitations as the population of a cell increases. Although not realistic, it has the advantage of simplifying the description and the coding of the model.

The interaction between amoebae and the environment obeys a stochastic law, and we consider that a non-empty *neutral* cell may become excited by with probability p_E called the *emission rate*. For $t \in \mathbb{N}$ and $c \in \mathcal{L}$, let \mathcal{D} be a Bernoulli function ; the interaction between amoebae and the environment is modelled by:

$$\sigma_c^{t+1} = M \quad \text{if } P_c^t > 0 \text{ and } \sigma_c^t = 0 \text{ and } \mathcal{D}(p_E) = 1 \quad (R7)$$

As rules R1 and R7 may interfere, we need to clear this ambiguity of formulation. A first possibility consists in according priority to rule R7 over rule R1. However, it is important to note that allowing this priority implies according a different meaning to the transmission rate p_T . As this probability was initially supposed to model uncertainty on receiving an excitation signal, we prefer to use a second

possibility, and to combine rule R1 and R7 into rule R1’:

$$\sigma_c^{t+1} = M \quad \text{if } \mathcal{B}(p_T) = 1 \text{ and } \sigma_c^t = 0$$

$$\text{and } \begin{cases} E_c^t > 0 \\ \text{or} \\ P_c^t > 0 \text{ and } \mathcal{D}(p_E) = 1 \end{cases} \quad (R1')$$

Rule R1’ states that a cell becomes excited with probability p_T if it is neutral and if it receives an excitation from a neighbouring cell or, with probability p_E , from the amoebae it contains.

To conclude the presentation of the model, we wish to call the reader’s attention on the fact that our description does not specify any type of neighbourhood. In the following, we will arbitrarily use the eight-cell neighbourhood, *i.e.*: $N_c = \{d \in \mathcal{L}, \max\{|d_x - c_x|, |d_y - c_y|\} = 1\}$. Note that it is not strictly equivalent to the Moore neighbourhood as cells are excluded from their own neighbourhood, and as cells in the border of the lattice \mathcal{L} have a smaller neighbourhood. We also arbitrarily set the excitation level to $M = 3$; the set of states is thus $\{0, 1, 2, 3\}$.

4 First analysis of the behaviour

Our method consists in examining the behaviour of the model from a qualitative point of view. We begin our study by simulating the evolution of a system for simple cases and examine the effects of changing the value of the parameter p_E , leaving the study of changing p_T and p_R for the next section.

4.1 Static fully deterministic case

First Experiment. We begin by examining what happens to a systems that contains only three amoebae in the fully deterministic case: the transmission rate and the emission rate are set to 1, the agitation rate is 0: $(p_T, p_E, p_R) = (1, 1, 0)$. Figure 2 shows the evolution of the system for these settings and a small lattice size $(30, 20)$. We observe that no chemotaxis ever occurs as excitation fronts do not hit the amoebae. Instead, we observe that when two excitations fronts meet, they simply annihilate.

Interpretation. Contrarily to classical diffusion waves, it is a well-known phenomenon that reaction-diffusion fronts annihilate when they meet. This property is respected by our model. It implies that the transfer of information may be limited to a certain part of the lattice. Let us define informally an *influence region* of an emitting cell as the set of cells that will receive the information emitted by this cell. Intuitively, we see that in the fully deterministic case, the influence regions of the amoebae correspond to the discrete Voronoi diagram of the lattice with amoebae as centre points (see Fig. 3 for an illustration and [2] for a more detailed analysis).

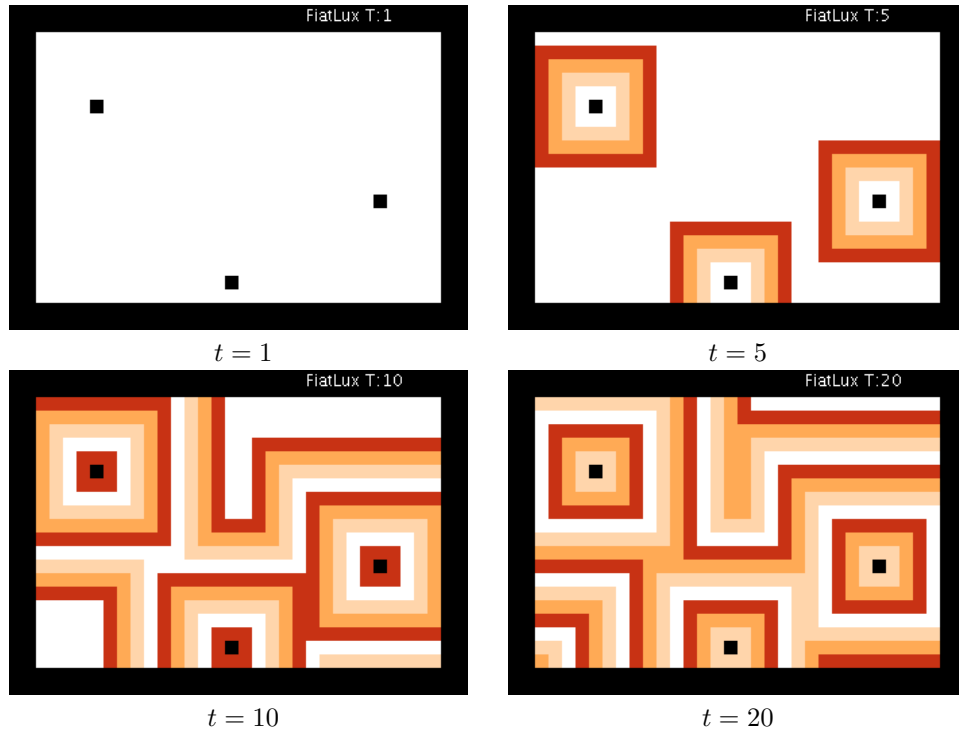


Figure 2: Four views of the evolution of the model with two amoebae in the fully deterministic case for a grid size $(30, 20)$ and $(p_T, p_E, p_R) = 1, 1, 0$. Amoebae are represented by black squares, white squares are neutral cells, darkest brown/grey squares are excited cells, lighter brown/grey squares are refractory cells. This colour code is kept in the following. All simulations are made with the *FiatLux* CA-simulator [8].

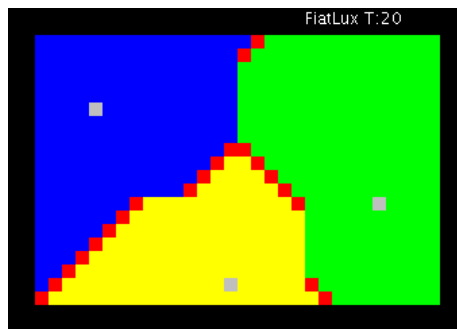


Figure 3: The corresponding regions of influence for each amoebae (see text). Diagonal frontiers are special cells that belong to two or three influence regions.

It is interesting to note that no communication between amoebae via the environment can occur in the fully deterministic case. Indirect communication can only occur when some amoebae become part of the influence region of other amoebae. Let us now examine if the gathering can be achieved by changing the value of the emission rate p_E .

4.2 Pacemaker Formation

Second Experiment. To illustrate the effect of changing the emission rate, we examined the behaviour of the system for the values $p_E \in \{0.01, 0.10, 0.50, 0.80\}$. To initialise the system, we assigned to each cell a 10% probability to contain an amoeba. Unless otherwise mentioned, we keep this random initial condition for all the following experiments ; this is compatible with experiments conducted by other authors (*e.g.*, [3]).

We experimentally observed that a gathering of amoebae occurs for all the values of p_E considered. Moreover, the smaller p_E was, the quicker the gathering happened. Figure 4 shows the evolution of the system for $p_E = 0.10$: a compact cluster emerges in a few hundred steps ; it emits waves with a good regularity.

To quantify the temporal gathering of amoebae, we propose to examine the temporal evolution of the *bounding box ratio* (BBR), defined as the ratio of the surface of the largest rectangle containing all the amoebae over the total surface of the lattice. More formally, for a given time t , if x_{\min}, x_{\max} (respectively y_{\min}, y_{\max}) are the minimal and maximal value of c_x (respectively c_y) such as $c = (c_x, c_y)$ and $P_c^t > 0$, then we have:

$$\text{BBR}(t) = \frac{(x_{\max} - x_{\min}) \cdot (y_{\max} - y_{\min})}{X \cdot Y}(t)$$

This parameter is rather simplistic since it captures only a small part of the system's organisation into clusters. However, we use it as a first step for quantifying the aggregation phenomenon, leaving improvements of this quantification for future work.

Figure 5 shows evolution of the BBR for different values of p_E . The first plot (top) displays the average evolution of for 50 independent samples. We see that, for the range of values considered, this evolution is regular ; it confirms the counter-intuitive fact that the gathering process is accelerated when p_E is decreased.

However, note that the smoothness of the curves comes from the averaging and does not describe the evolution of a single sample. The second plot of Fig. 5 (bottom) shows the evolution of a single samples for three values of p_E . The particular curve obtained for $p_E = 0.5$ is interesting since it shows three stages. By looking at the evolution of the patterns, we observed that these three stages correspond to:

- for $t \in [0, \sim 500]$ amoebae reorganise to form two unstable clusters,

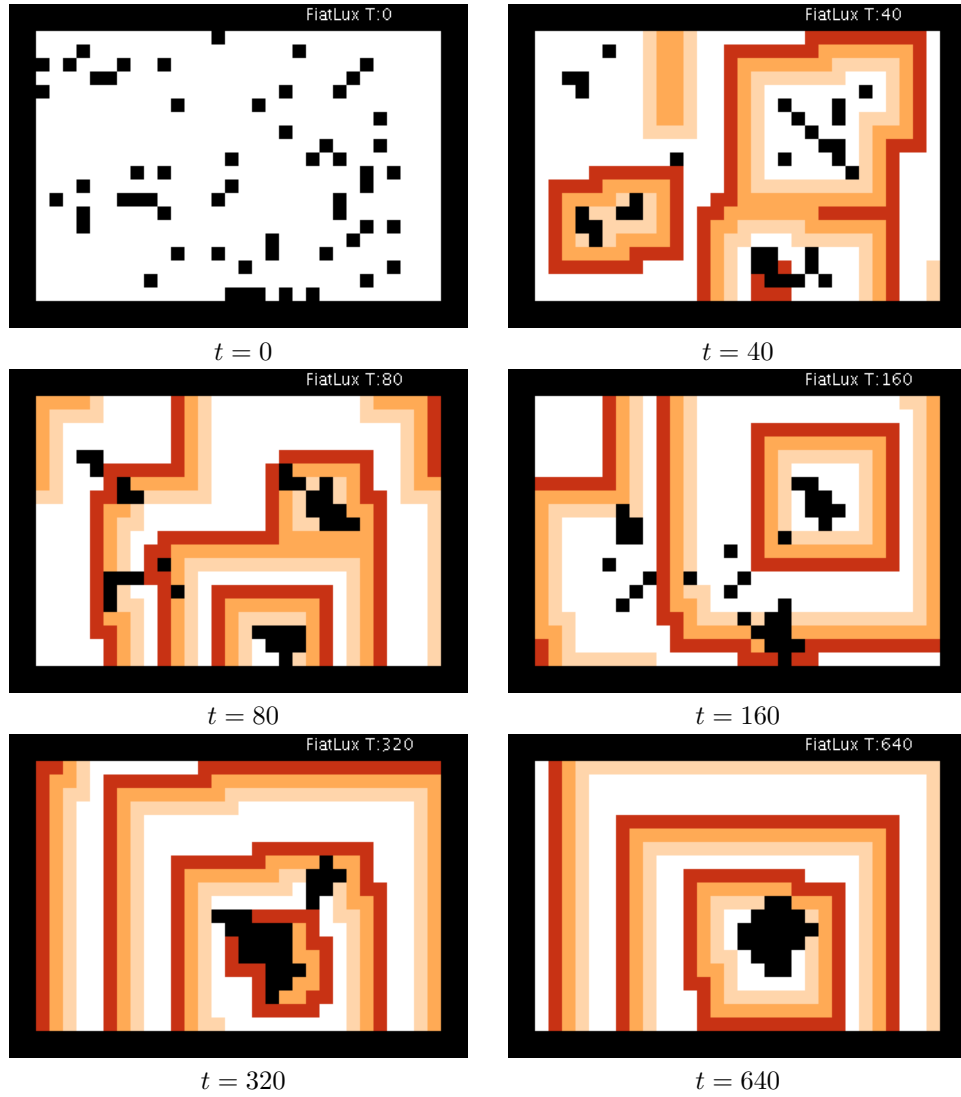


Figure 4: Sequence showing the formation of a pacemaker with $(p_T, p_E, p_R) = (1, 0.10, 0)$ and $(X, Y) = (30, 20)$.

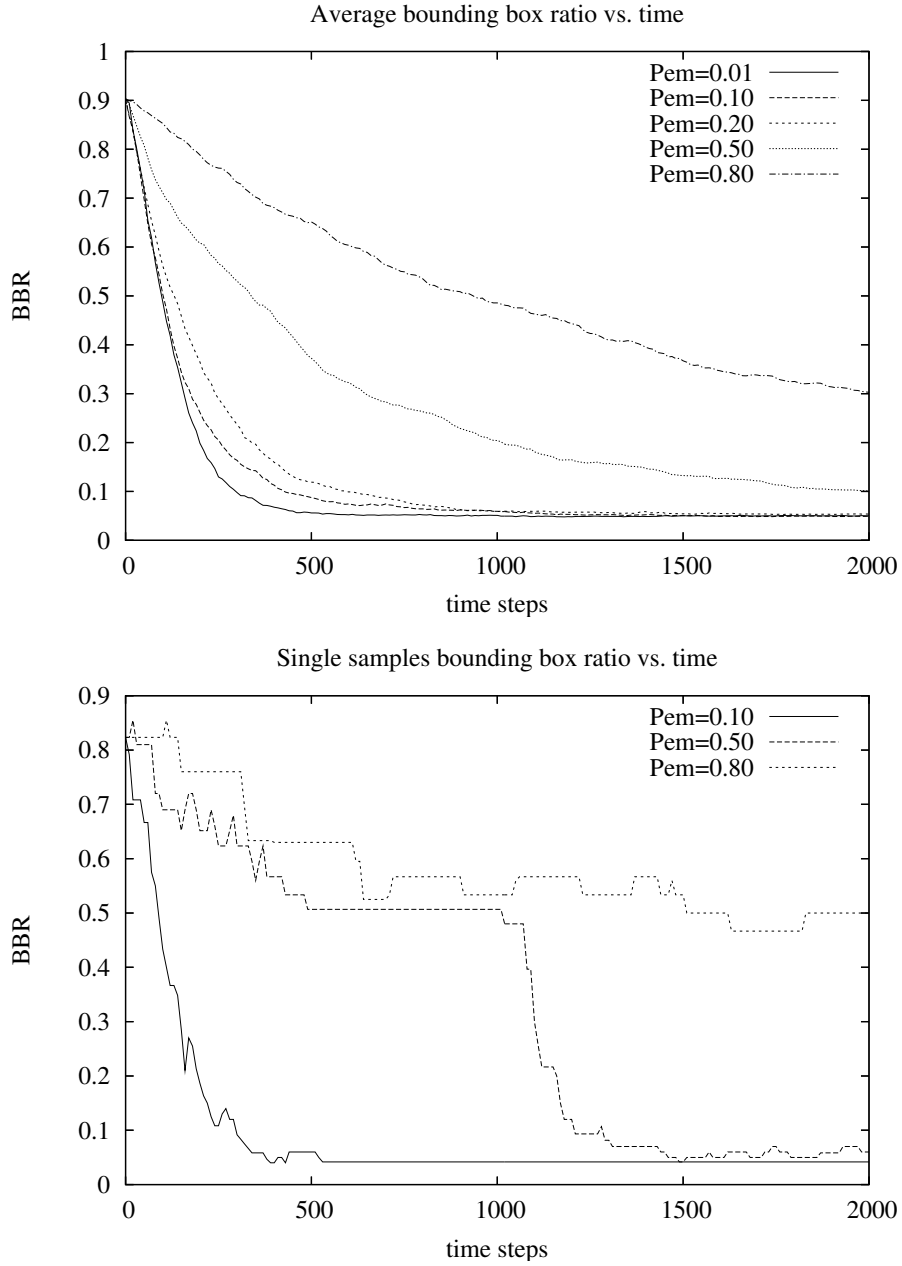


Figure 5: Evolution of the bounding box rate (BBR) as a function of time for a grid size $(30, 20)$, $p_T = 1$, $p_R = 0$, and different values of p_E . Average evolution for 50 samples (top) Example of a single sample evolution (bottom).

- for $t \in [\sim 500, \sim 1000]$ the two clusters emit excitation fronts with an irregular pace, during this stage, influence regions of the two clusters shrink or extend due to the irregularities of emissions,
- for $t > 1000$ one of the two clusters, the “winning cluster”, have its influence region touch the other cluster, the “loosing cluster”: the amoebae flow from the loosing cluster to the winning one and finally form a single cluster.

Interpretation. For small lattices, the decrease of p_E allows the system to achieve decentralised gathering. The organisation of the system is initiated when randomly chosen cells emit an excitation wave which will attract other non-emitting cells to it. The repetition of the process creates more populated regions of the lattice. These dense regions or *clusters*, examined as a whole, emit excitation waves and attract the cells that are in their influence region. The more a cluster increases in size, the more regularly it emits excitations: this results from the fact excitations on one cell are independent from the other cells. This correlation between the size of a cluster and its frequency of emission creates a positive feedback ; at the end, all cells gather in the same cluster. If this cluster has a reasonable size, it emits waves with a good regularity ; by analogy with the biological phenomenon, we can call it a *pacemaker* (e.g., [7]).

4.3 Gathering on Larger Lattices

How does this self-organising system behaves for larger lattices and for a great number of amoebae? We now to examine how the self-organisation process is structured, how several pacemakers merge to form one or several clusters.

Third Experiment. Keeping $p_T = 1$ and $p_R = 0$, we repeated the previous experiment with a lattice size $(150, 100)$ and for an observation time of 40 000 time steps. Fig. 6 shows one evolution of the system for these settings. Repeating this experiment for 100 random samples, using the bounding box rate measures, we observed that the system achieves the decentralised gathering task within this period of observation (see also Fig. 8 p. 17).

Moreover, observing some simulations, we noticed many surprising effects that can only be observed on large lattices. For example, it happened that some clusters are destroyed when they enter the influence regions of another cluster but spontaneously reformed when the attracting cluster, by “chance”, shrinks its influence region. There are also rare cases where a cluster divides into two, one part being attracted by a different cluster, the other part by another different cluster. Looking at Fig. 6, one might notice that the streams are orthogonal and follow the four diagonal axis. As mentioned earlier, we believe that this effect is due to the choice of the neighbourhood. Using our simulation software, we observed that diagonal effects can be overcome by choosing a circular neighbourhood [21].

Interpretation. The self-organisation of amoebae is a phenomenon that displays good scaling properties. The gathering of amoebae into clusters is a result

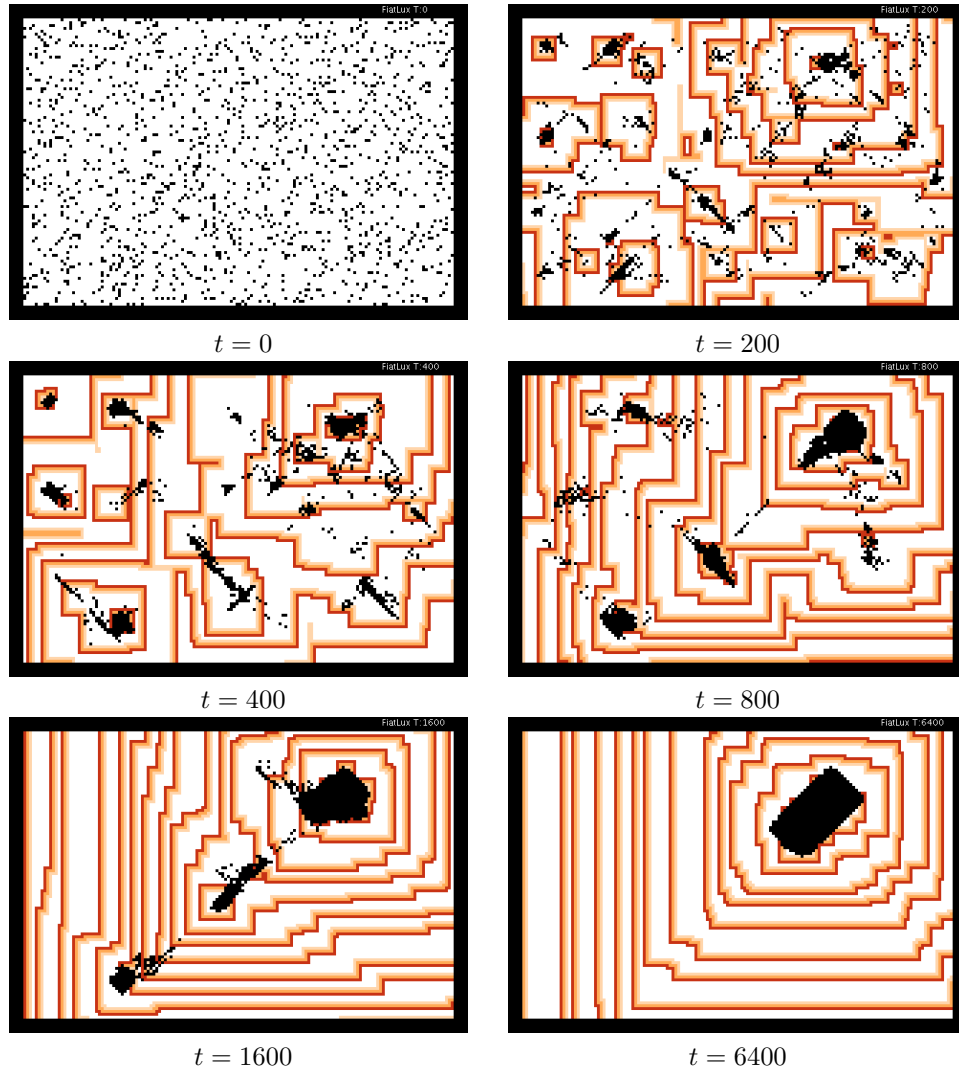


Figure 6: Evolution of the model with perfect transmission rate and no agitation: $(p_T, p_E, p_R) = (1, 0.01, 0)$.

of captures of one cluster by another cluster, or possibly two. When two pacemakers compete for extending their influence region, we observe that the bigger one has a tendency to win. Indeed, as amoebae emit their waves independently, the bigger the size of a pacemaker, the larger the probability to emit a wave. So all happens as if each pacemaker had an “average frequency of emission” that separates two departures of waves. Informally, we can notice that when the size of a group becomes big enough, this average frequency approaches $1/M$, *i.e.*, we are close to the fully deterministic case.

When the waves are not regularly emitted, the influence regions extend or shrink according to where the excitation fronts meet. We intuitively perceive that, in average, when two neighbouring pacemakers having two different average frequencies of emission “compete”, the pacemaker that has the highest frequency sees its influence region extend while the other pacemaker sees its influence region shrink.

Once a pacemaker has its influence region eliminated, the cells come under the influence of another pacemaker and they converge towards this pacemaker by forming streams. It is interesting to note that these streams are also observed in *in vitro* experiments on *Dictyostelium*.

5 Robustness to perturbations

Now that we have established that the gathering is possible by decreasing the value of p_E , we try to estimate the robustness of the model changing the value of p_T and p_R . We examine how the model resists to three types of perturbations: transmission faults on the environmental layer, randomness imposed on the moves of the amoebae and introduction of obstacles on the lattice.

5.1 Self-organisation with agitation

Fourth Experiment. In order to examine whether the system is robust to noise superimposed in the moves of the amoebae, we set the agitation rate to 10%, keeping the two other parameters unchanged: $(p_T, p_E, p_R) = (1, 0.01, 0.1)$. Figure 7 shows one evolution of the system for these settings and Fig. 8 shows statistical measures obtained for different values of p_E and p_R . It is remarkable that the addition of $p_R = 20\%$ of random move does not slow much the gathering process. For higher values of p_R the perturbations are too important to allow compact and stable clusters to form ; however a form of gathering can still be observed, at least for p_R smaller than 0.5.

Interpretation. The gathering still occurs even when the moves of the amoebae are perturbed by a small amount of noise. The most noticeable difference in the dynamics is that groups of small size do not appear. This tends to show that there exists a link between the stability of groups of a given size and the parameter p_R . Finding a relationship between the minimal group size (if such a property exists) and the quantity of noise is another interesting question that arises from these observations.

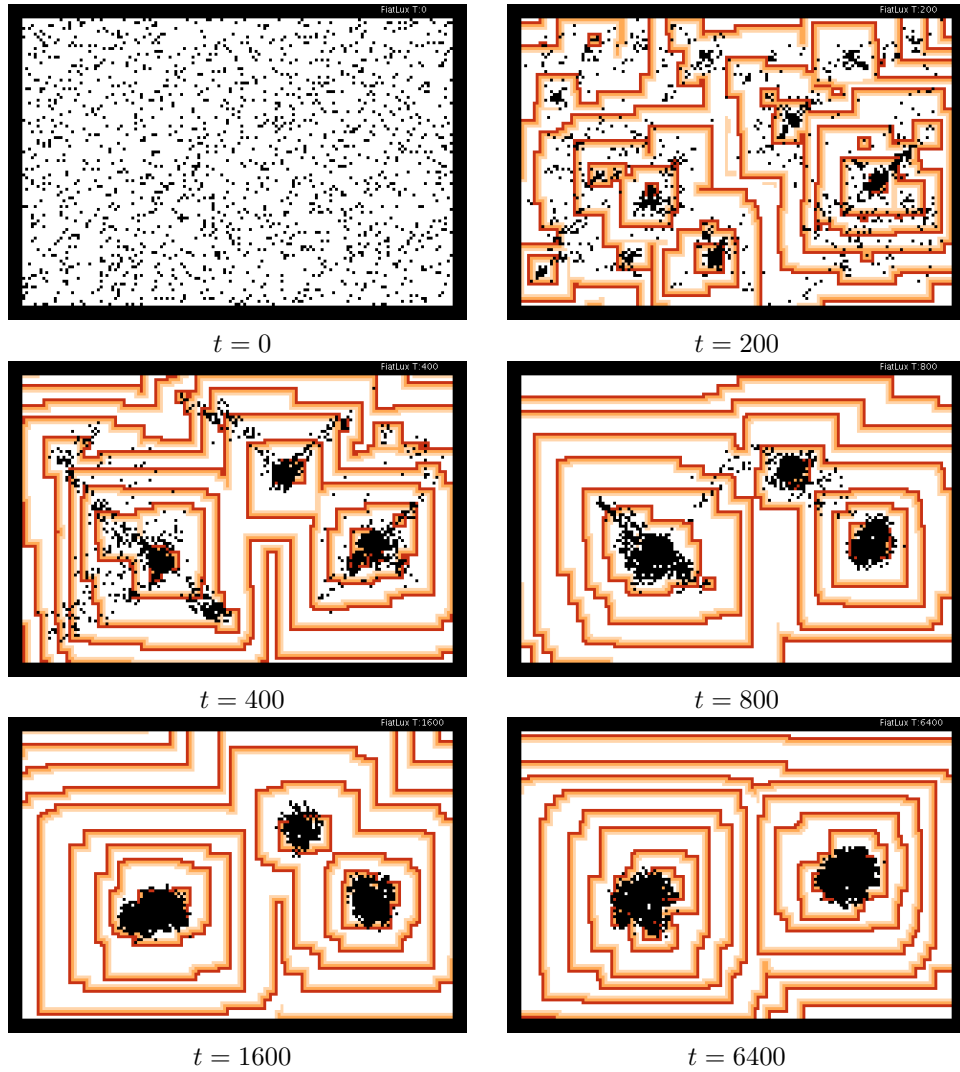


Figure 7: Evolution of the model with perfect transmission rate and small agitation: $(p_T, p_E, p_R) = (1, 0.01, 0.1)$.

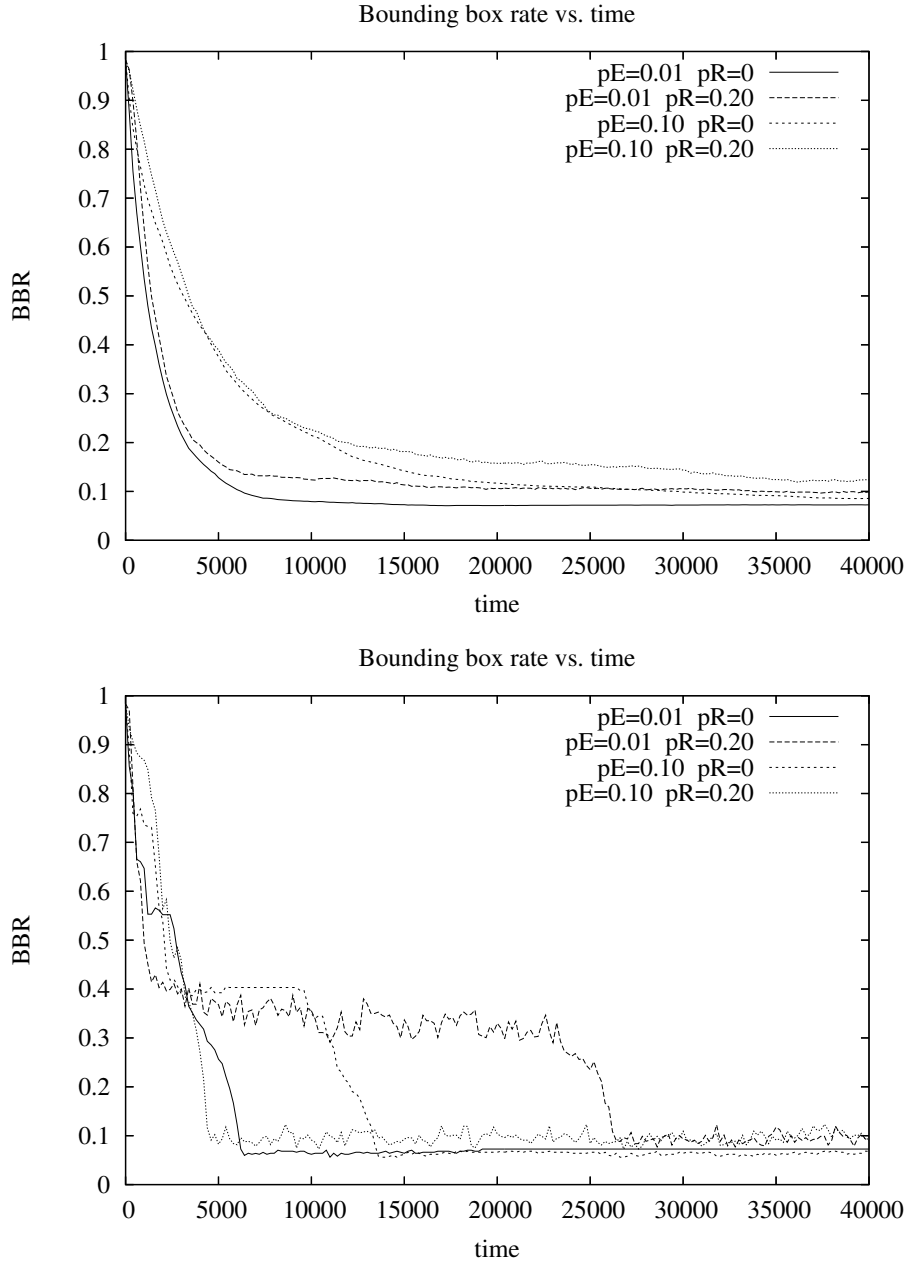


Figure 8: Evolution of the BBR as a function of time for a grid size (150, 100), $p_T = 1$, and different values of p_E and p_R . Average evolution for 100 samples (top) Example of a single sample evolution (bottom).

5.2 Obstacles on the lattice

Fifth Experiment. It is interesting to consider what happens to the system when the topology of the lattice is no longer regular. In particular, how do amoebae operate when obstacles are introduced? This question is particularly important if we are to apply the coupling of reaction-diffusion and chemotaxis to guide robots in real environments. It is also interesting to note that real amoebae evolve in very inhomogeneous media and also need to achieve the gathering despite the presence of numerous obstacles.

In Fig. 9, we present the evolution of the system where obstacles (straight lines) are placed randomly on the lattice. Obstacles do not allow information nor amoebae to cross.

Interpretation. We notice that the system behaves very well in the presence of obstacles. In the parts that are totally disconnected from the rest of the lattice, isolated groups are formed. In the others parts of the lattice, the aggregation process is not perturbed by the presence of obstacles. In particular, in some parts of the lattice, it is possible to observe the amoebae taking narrow spaces to converge to a pacemaker. In this case, the streams formed are thin and they usually split and re-form several times before reaching a pacemaker. It is interesting to notice that this type of robustness is obtained “for free”: it can be seen as a an emergent property since at no time it was explicitly coded in the local rules governing the agents and the environment.

5.3 Loss of coherence in the propagation of fronts

Sixth experiment. We now set the transmission rate to $p_T = 0.98$, *i.e.*, we introduce a 2% chance that a cell fails to receive an excitation. The evolution of the system is shown on Figure 10. We see that for small times the system behaves qualitatively in the same way as for the non-perturbed case: waves are initiated by amoebae, they propagate until they collide and annihilate. However, as transmission errors accumulate, the waves become more chaotic ; they progressively loose their coherent circular shape. After a few hundred steps, spiral waves appear and become persistent, independently of the amoebae. As time advances, more and more persistent spiral waves appear. When the coherence is totally lost, amoebae start moving as they sometimes receive excitation fronts. However, their moves are erratic since the positions of the fronts are independent of the positions of other amoebae.

Interpretation. The presence of small transmission errors in the environment may create situations were spiral waves can survive arbitrarily long periods of time. The multiplication of such waves causes confusion in the system and does not allow the amoebae to group into clusters. We call this behaviour where waves can develop independently of the position of the amoebae, the *non-coherent regime*. The very existence of this regime underscores a possible weakness of our model: if the medium on which the reaction-diffusion is implemented is not perfect, the aggregation process may fail.

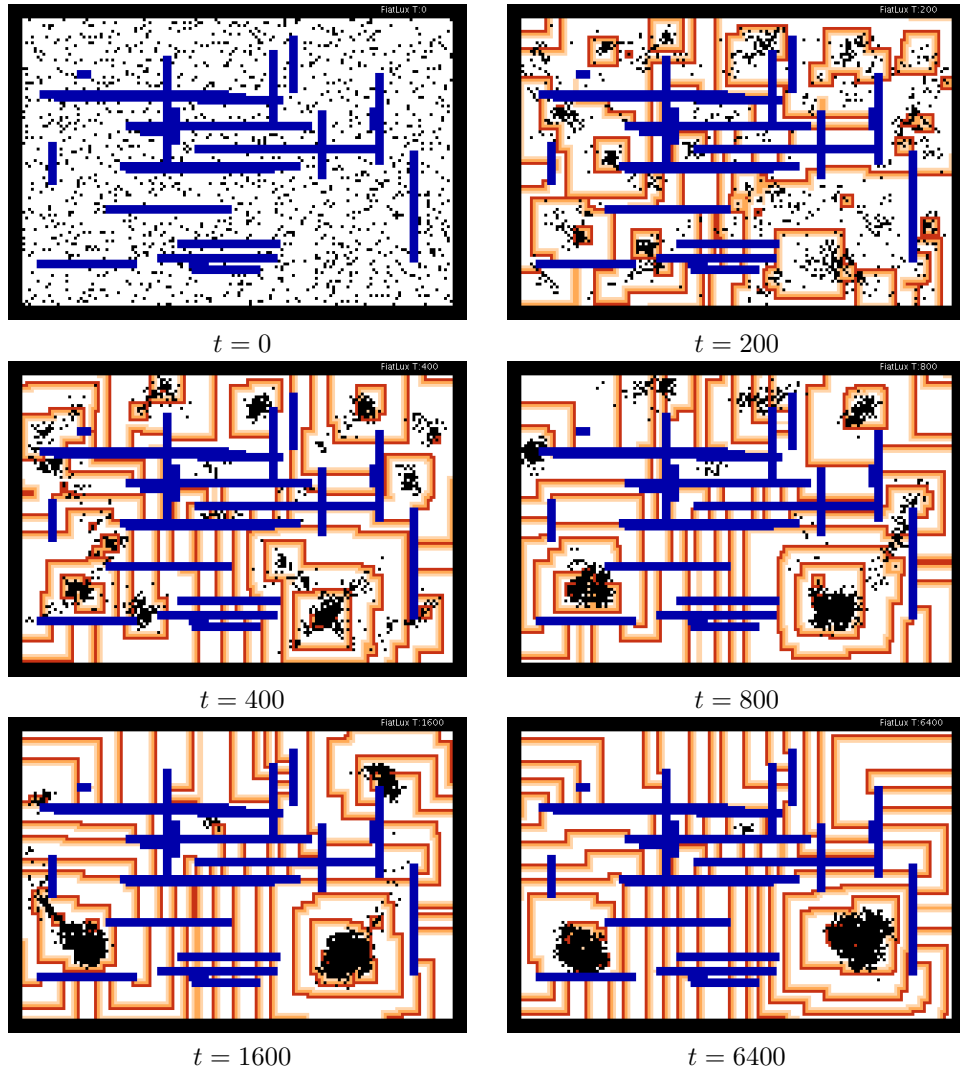


Figure 9: Evolution of the model with obstacles, perfect transmission rate and small agitation: $(p_T, p_E, p_R) = (1, 0.01, 0.1)$.

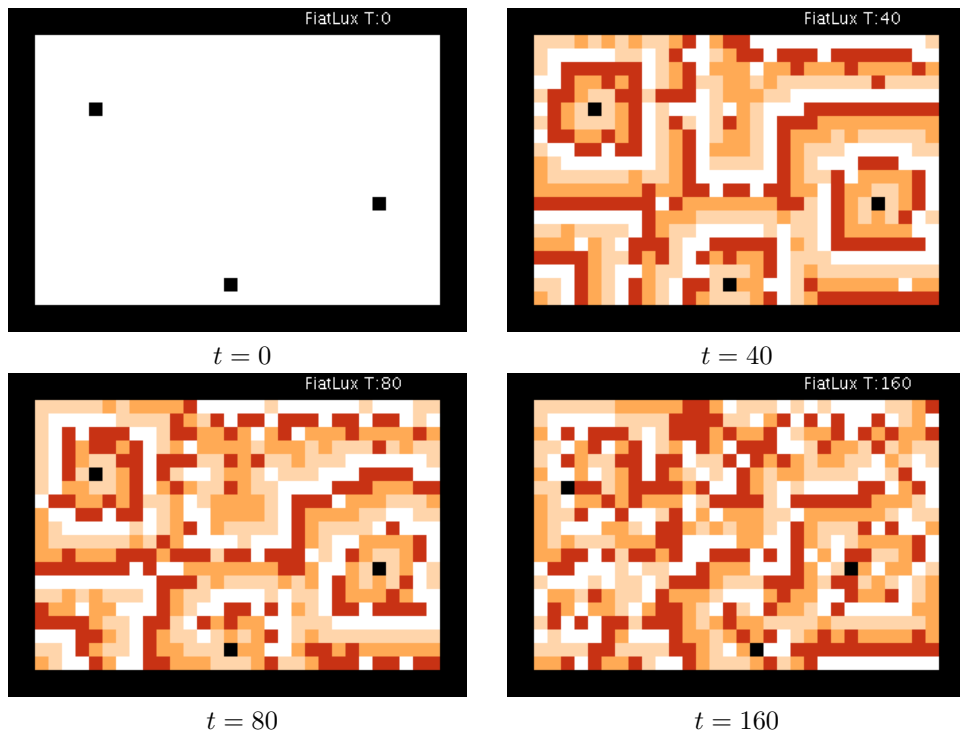


Figure 10: Loss of coherence occurring with non-perfect transmission rate: $(p_T, p_E, p_R) = (0.98, 1, 0)$, small lattice of $(30, 20)$.

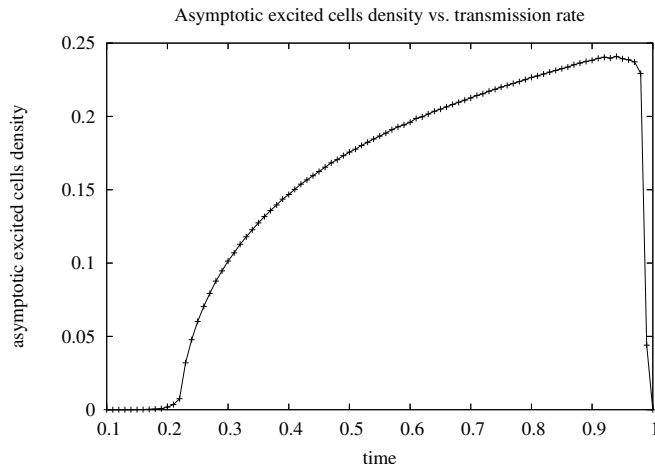


Figure 11: Evolution of an environment depleted of amoebae with initially 10% cells set in the excited state. Average value of the asymptotic density of excited states (see text). Lattice size is (100, 100).

5.4 Extinction of the self-entertained waves

For smaller values of p_T the loss of coherence is observed even more rapidly. Interestingly enough, when the transmission rate is small enough, we observed that the spiral waves were no longer persistent. We call this new qualitative behaviour, where spiral waves spontaneously disappear, the *extinction regime*. We experimentally observed that the transition from the non-coherent regime to the extinction regime is sharp and occurred for $p_T \sim 0.22$.

Seventh Experiment. In order to understand the origin of this abrupt change of behaviour, we examined what happened to a system depleted of amoebae, where some cells were artificially set to the excited state. To separate the non-coherent regime from the extinct regime, we monitored the evolution of the density of excited cells:

$$e(t) = |\{c \in \mathcal{L} \mid \sigma_c^t = M\}|/X.Y$$

We expect this quantity to reach quickly zero for the extinction regime and to remain strictly positive for the non-coherent regime.

We varied the transmission rate p_T by 1% steps from 0.01 to 1. For a lattice size (100, 100), the system was initialised with no amoebae on it and with cells having a probability of 10% to be the *excited* state, otherwise left in the neutral state. We measured the evolution of the $e(t)$ during $T = 10^4$ time steps. For each value of p_T , this experiment was repeated with 50 random samples. For each sample, we computed the approximation of the asymptotic density of excited cell, *i.e.*, for each sample, we measured the average value of

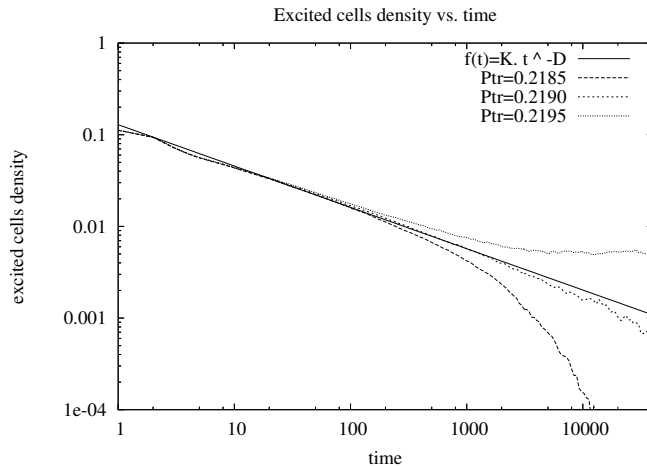


Figure 12: Evolution of an environment depleted of amoebae with initially 10% cells set in the excited state. Grid size is (800, 800). Average density of excited cells as a function of time for different values of transmission rates, displayed in a log-log scale.

$e(t)$ for $t \in [10^3, 10^4]$. We then extracted the average and standard deviation of the distribution of these measures.

Figure 11 shows this average as a function of p_T . We observe that for $p_T < 0.96$, the shape of the curve is regular. The standard deviation measured did not exceed 10^{-3} , so errors bars would be smaller than the thickness of a line.

Interpretation. The shape of the curve suggests that the transition between the two regimes is a second-order phase transition that occurs for $p_T \sim 0.22$. We can also note that for p_T close to 1, we observe a non-regular behaviour that is due to finite size effects: because of the limitation of the grid, the probability of apparition of persistent spiral waves is small and the non-coherent regime may not be reached. This means that for values of p_T close to 1, the system oscillates between the static behaviour described in section 4.1 and the non-coherent regime described in the previous section.

Refining the previous experiment. To analyse the nature of the change near criticality, we monitored the evolution of $e(t)$ for the transmission rates $p_T \in \{0.2185, 0.2190, 0.2195\}$. For different lattices sizes, up to (800, 800), the average value of $e(t)$ was measured for 50 random initial samples. We observed that this small variation of p_T , of the order of 10^{-3} , separated a behaviour where the system quickly converges to the extinction regime from the non-coherent behaviour where excitations survive arbitrary long periods.

Moreover, plotting the average value of $e(t)$ for different lattice sizes, it appeared that the curved closely followed a power-law. It is well known in

Table 2: Synthetic view of the qualitative behaviours observed by simulating the aggregation model

p_E	p_T	p_R	qualitative behaviour
1	1	0	static
[0.2, 1]	1	0	self-organising (slow)
[0.01, 0.2]	1	0	self-organising (quick)
[0.01, 0.2]	1	0.2	self-organising (quick)
[0, 1]	[0.23, 1[0	non-coherent
[0, 1]	< 0.22	0	extinct

statistical physics that the power laws observed in phase transitions are not arbitrary: there are particular sets of exponents that characterise the evolution of the system near criticality. The class of different phenomena that can be described by the same sets of exponents is called a *universality class*.

By analogy with previous observations made in asynchronous cellular automata, we made the hypothesis that the phase transition belonged to the universality class of *directed percolation* [4, 9]. This allows us to predict that if this hypothesis is correct, the evolution of excited cells density follows $e(t) \sim t^{-\delta}$ near criticality. The value of the dynamical exponent of directed percolation is $\delta = 0.541$ in the two-dimensional case ; this number is known only experimentally [12]. Fig. 12 shows the evolution of the average value of $e(t)$ for a grid size (800, 800). We see that, as expected, for $p_T = 0.2190$, the slope of the power-law in a log-log plot closely follows the predicted value.

Interpretation. The observations made for the environment layer are strongly similar to those observed in asynchronous elementary cellular automata as the evolution of $e(t)$ near criticality obeys to a second order phase transition. A first estimation suggests that the universality class of the phase transition is directed percolation. This rises the question to determine what are the links between these two types of models. It can also give us a hint on how real amoebae collectively decide to start the gathering phase. Although there are huge differences between the biological system and our simplistic model, it might be possible to examine whether they involve the same principles. Another nice problem consists in taking advantage of these phase transitions for designing artificial decentralised consensus, for example for achieving a self-diagnosis task. We can imagine that a network of interconnected sensors decides to change its behaviour when a critical fraction of defective components is reached.

6 Conclusion and perspectives

The model we proposed to achieve decentralised gathering is inspired from the aggregation phenomenon in *Dictyostelium*. It uses a simplified reaction-diffusion mechanism to propagate information and a chemotaxis law to direct the moves of the virtual agents. The set of experiments we presented showed that the

dynamics of the system is rich. Four different qualitative behaviours were exhibited: the static regime, the self-organising regime, the non-coherent regime, and the extinction regime (see Table 2).

The self-organising regime was examined under various conditions. It was shown that, by using only four states and by varying one probability, it was possible to efficiently solve the problem of achieving a decentralised gathering by using only local rules. We showed that the dynamics of the process, far from trivial, consisted in a progressive merging of groups, from small groups to large groups. We proposed to interpret this hierarchical organisation as a result of different emerging behaviours:

1. formation of waves,
2. formation of first clusters that act as pacemakers,
3. the apparition of a frequency of emission that becomes higher as the size of the clusters increases,
4. extension and shrinking of the influence regions of clusters according to their respective size,
5. capture of small clusters by larger ones.

Among interesting properties observed in the system, it was shown that the gathering could also occur in the presence of noise on the moves of the amoebae. Moreover, when obstacles were introduced, the gathering was not much perturbed as the virtual amoebae could take advantage of narrow corridors to find their way to a pacemaker.

It is interesting to compare this model to other bio-inspired models that use virtual chemotaxis such as virtual ants (*e.g.*, [5]). Virtual ants use simple diffusion and chemotaxis to realise complex tasks in a decentralised way. It would be interesting to determine the pros and cons for using each of the two models. At first sight, the main advantage of our reaction-diffusion-chemotaxis model is the small number of states it uses (here only four).

On the other hand, we showed that the model was not robust to noise on the environment. This hypothesis is not restrictive in a computer science context where computing components are almost perfect, but it may be more problematic in situations where the components may be defective. So one of the challenges that arises from our work is to find whether another model of reaction-diffusion-chemotaxis can be designed that would still ally simplicity of the rules and the resistance to perturbations of the agents, but would also be applied in a defective environment.

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