CA-like Simulations of Dynamic Neural Fields

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Abstract

The paper describes the application of cellular-automaton-like simulations to dynamic neural fields. Dynamic neural fields show a complex dynamic behaviour which has been investigated successfully by analytical methods so far only for the one-dimensional case. We concentrate our interests mainly to simulations of two spatial dimensions and their different dynamic patterns. In two examples we apply dynamic neural fields to problems in computational neuroscience.

1 Introduction

In modelling neuronal spatially distributed phenomena one can generally choose two different ways (*cf.* [11]): One way is to setup a network of discrete model neurons and all their interconnection weights, which is usually done in the so-called PDP approach ([18, 12]). The main interest lies on the learning capabilities of the established network, i. e. on the correct adaptations of the connection weights. Another approach to neuronal modelling is using continuous networks (so-called fields). The number of neurons is unlimited in these models, and the connections between the neurons are handled in a general way (e. g. statistically) without having individually changing weights. Therefore, instead of being interested in the learning mechanisms of the network one investigates the dynamics of activity of the fields. It is a convenient way to describe the evolution equations of the field by integro-differential equations (IDEs).

One important class of continuous networks are dynamic neural fields (DNFs). DNFs were first introduced by Amari [1]. Similar formulations are made in [2] and [13]. This paper is motivated by two efforts. Firstly, we want to describe a method for simulations of two-dimensional DNFs and secondly, we show their use to two different problems in computational neuroscience.

Amari [1] investigated a model of DNFs as a set of IDEs and could found solutions for the one-dimensional spatial case. However, most spatio-temporal computations of mammalian brains involve more than one spatial dimension. Therefore we present a method to simulate two-dimensional DNFs which is based on cellular automata (CA) simulations used for reaction-diffusion systems. The simulations offer a powerful way to investigate qualitatively the dynamics of the spatio-temporal patterns described by the IDEs. Further they can be used in applications of modelling biologically motivated space-time computations.

In the next section we look shortly at the results of the work of Amari. Then we give details of our own simulations for two-dimensional DNFs. In Section 4 we discuss the usefulness of our method. We show on two examples in Section 5 the application of the approach to problems in computational neuroscience. The following last section concludes the paper.

2 Dynamic neural fields

Usually one regards DNFs as spatially distributed populations of model neurons which are connected in a random manner (*cf.* Amari [1]). Being more precisely one can distinguish different layers of neurons of the same type. The average intensity connection function is of the lateral inhibition type.

Let us consider m two-dimensional neuronal layers fully connected. The average membrane potential of the neurons in the ith layer at position $\mathbf{x} = (x_1, x_2)$ and time t is $u_i(\mathbf{x}, t)$. The general field equations (1) incorporate a sigmoid activation function f_i, a (usually negative) value h_i as a resting potential, an external stimulation function $s_i(\mathbf{x}, t)$, and a connection function $w_{ij}(\mathbf{x})$ which gives the strenght of the influence of neurons from layer j to the i-th layer at place $\mathbf{x}$:

$$\tau_i \frac{\partial u_i(\mathbf{x}, t)}{\partial t} = -u_i + \sum_{j=1}^{m} \int_{-\infty}^{\infty} w_{ij}(\mathbf{x} - \mathbf{x}^*) f_j[u_j(\mathbf{x}^*)]\, d\mathbf{x}^* + h_i + s_i(\mathbf{x}, t). \quad (1)$$

From a mathematical point of view it is clear that one cannot analyse this system of equations for general functions of f,w, and s. In a first step Amari made the following simplifications: The sigmoid functions f_i are simplified to a step function:

$$f[u] = \begin{cases} 1, & \text{if } u > 0 \\ 0, & \text{if } u \leq 0, \end{cases} \quad (2)$$

which means, that the field at a certain place is only for $u > 0$ in the excited state[1].

The connection function w is supposed to be symmetrical and homogeneous, i. e. $w(\mathbf{x}) = w(-\mathbf{x})$. The stimulation function s is kept constant. Although these constraints simplify the investigations it is however still an difficult task to analyse the system due to the great complexity of (1) and different initial values of the fields u_i. The simplest case is an one-dimensional field consisting of one layer.

2.1 DNF of one spatial dimension

For the case of one neural layer,

$$\tau \frac{\partial u(x,t)}{\partial t} = -u + \int w(x-x^*) f[u(x^*)]\, dx^* + h + s(x,t), \qquad (3)$$

Amari proved the existence of five types of pattern dynamics:
- monostable field in which all excitations will die out
- monostable field which is entirely excited
- (explosive type) bistable field in which localised excitations up to a certain range spread without limit over the entire field, but vanish if the range is to narrow
- bistable field in which initial excitations either become localised excitations of a definite length or die out; localised excitations move in direction to the maximum of the input s
- fields shows spatially periodic excitation patterns depending on the average stimulation level.

The type of dynamics of a field depends mainly on the connection function w. For a mexican hat type connection function, also known as difference of two gaussians (Fig. 1), one assumes that excitatory connections dominate for proximate neurons, and inhibitory connections dominate at greater distances. This type is also known as a lateral inhibition type. In particularly, the positive range of $w(x)$ along the x-axis determines the length of excited ranges of $u(x)$.

The complexity of dynamics increases if one adds a second layer to the field u. Apart from the types mentioned for the case of one layer one can further detect oscillatory patterns and traveling waves. Amari simplified (1) in order to cope with the analysis of both fields in the following way: one layer, say u_1, is a layer consisting of only excitatory neurons, and the other layer, say u_2, consists only of inhibitory neurons. Moreover, one can restrict the connections so that the inhibitory neurons only inhibit the excitatory neurons and the excitatory neurons have very narrow fan-out connections to the inhibitory neurons. The latter can mean that the excitatory neurons at place x excite the inhibitory neurons at place x only.

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[1] In [10], Amari showed that the following results hold also for smooth sigmoid functions.

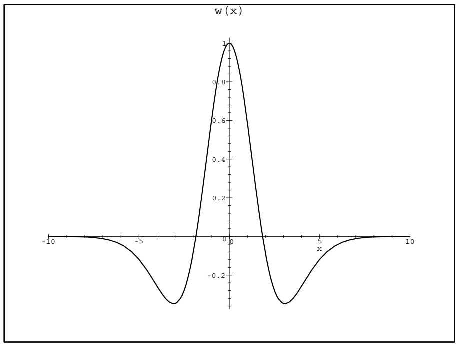

Figure 1: The one-dimensional connection function $w(x)$.

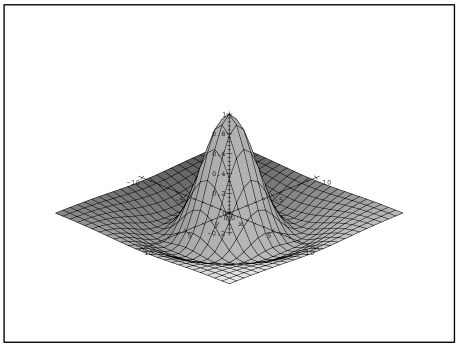

Figure 2: The two-dimensional connection function $w(\mathbf{x})$.

Thus, the field equations turn out to be:

$$\begin{aligned}
\tau_1 \frac{\partial u_1(x,t)}{\partial t} &= -u_1(x) + \int w_1(x-x^*) f[u_1(x^*,t)]\, dx^* \\
&\quad - \int w_2(x-x^*) f[u_2(x^*,t)]\, dx^* + h_1 + s_1(x,t) \\
\tau_2 \frac{\partial u_2(x,t)}{\partial t} &= -u_2(x) + w_3 f[u_1(x,t)] + h_2 + s_2(x,t). \qquad (4)
\end{aligned}$$

Note, that in Equations (4) the functions w_1 and w_2 are now of the gaussian type and w_3 is a constant.

A travelling wave across the field can be established as follows: Suppose a localised excitation in u_1 at position x and an localised excitation in u_2 at position $x+\epsilon$. The value of ϵ depends on the significant range of w_1 and w_2. The excitation in u_2 prevents in u_1 the propagation of the excitation in both of the two directions[2]. Therefore, the excitation in u_1 moves in the opposite direction, compared to the placement of ϵ. If the maximum of the first excitation is moved far enought the excitation in u_2 will inhibit the previously excited regions in u_1. The excited region in u_2 will follow the travelling wave in u_1. This process without external stimuli s keeps on indefinitely.

Here we cannot discuss in greater detail the analysis made by Amari (but see also [20]). However, one can assume that more complex systems than in Equations (3) and (4) are analytically intractable. There are two major ways to overcome this situation. On the one hand, one can calculate solutions of certain cases of (1) numerically in a direct fashion, or on the other hand, one can simulate the evolutionary equations. We decided to take the second way, because direct numerical calculations may still be too complex or are not very suitable to indicate the temporal evolution of the dynamic patterns.

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[2] An excitation in the layer u_2 indicates that the field at this position is in the refractory state.

3 Simulations of DNFs in two spatial dimensions

If one looks for solutions of the DNF equations for the two-dimensional case one may suppose to find in general the same types of dynamics as Amari found for the one-dimensional fields. In this section we reproduce different dynamic patterns of two-dimensional DNFs. This is mainly done by showing pictures of neuronal layers at different discrete times.

3.1 The simulation method

In our approach we have adopted the way of CA-simulations for reaction-diffusion systems (see e. g. the work of Gerhardt et al. [5, 6, 7, 8, 9] and the papers by Weimar et al. [23, 24]). In these methods time and space of the equations were discretised in order to find a limited number of possible states of the medium. In contrast to common cellular automata they had to choose larger neighbourhoods with different weights. This is more realistic because diffusion is not restricted to the nearest neighbours, and, on the other hand, the amount of diffusion decreases with greater distance.

A more straightforward approach is to rewrite the evolutionary equations (e. g. (1)) as as set of difference equations. Then, one can use for the field variable u numerical values of a certain range. The convolution term $\int w(x)f[u(x)]dx$ will be threated as a sum: $\sum_{k=-r}^{k=r} w(k)f[u(x+k)]$. For example, Equation (3) can be rewritten as a difference equation in the above sense:

$$u_i^{t+1} = u_i^t + \frac{-u_i^t + \sum_{k=-r}^{r}(w_k f[u_{i+k}^t]) + h + s_i^t}{\Delta t \tau}. \qquad (5)$$

Note, that the lower index indicates a position in space and the upper index is a discrete moment in time. Of great interest will be the value of r, which is the range of the neighbourhood. If r is relatively small, than the calculations will be faster compared to greater values of r. Ideally, r should be large (ranging over the entire field) to ensure, that the difference equations are as similar as possible to the differential equations. Of course, by doing the simulations one should find a good compromise: the value of r can be decreased as long as the qualitative behaviour of the dynamics doesn't change significantly. Equation (5) can be easily generalised to express the difference form of Equations (4). But one should be aware that the calculations for the neighbourhood for more than one layer are more time consuming.

Before we look in detail at the simulation results we address a last question in this respect: How one should deal with the boundary of a field. There are two major methods of traditional CA-simulations. Either one thinks of the field as a circle (in one dimension) or as a torus (in two dimensions). Or, on the other hand, one applies the zero-flux boundary condition, which states that there will be no influence to border cells from the outside. For all the following simulations we used the second point of view.

3.2 Single-layered DNFs

Our field consists of 100x100 discrete points, stored in a matrix **U**. The connection function is stored in another matrix **W** and the input in matrix **S**. The values for the elements of **W** are generally calculated by the function $w(\mathbf{x}) = w(x_1, x_2)$:

$$\begin{aligned} w(x_1, x_2) \quad &= \quad a_1 * exp(-(x_1)^2/\sigma_1 - (x_2)^2/\sigma_1) - \\ & \quad\quad a_2 * exp(-(x_1)^2/\sigma_2 - (x_2)^2/\sigma_2), \end{aligned} \tag{6}$$

which is a two-dimensional mexican hat (Fig. 2). The range for x_1 and x_2 depends on r (see Equation (5)).

In the following figures[3] we show some pattern formation processes of different dynamic types. Qualitatively, in the two-dimensional case of one-layered DNFs one finds the same types of pattern dynamics as in the one-dimensional case (*cf.* [20]). In Fig. 3 we have two initial excitations of different diameter. The larger one dies out whereas the smaller one survives due to the nearly same sized positive (excited) region as the connection function w. Note, the two excitations don't influence each other, because r is small. One interesting feature of DNFs is the support of converging and coexisting excitations (Fig. 4). This becomes important in modelling short term memory functions of the brain by layered neuronal tissue. A richer dynamic emerges if one gets rid of the homogenity of the field, e. g. by introducing asymmetric connection functions as shown in Section 5.

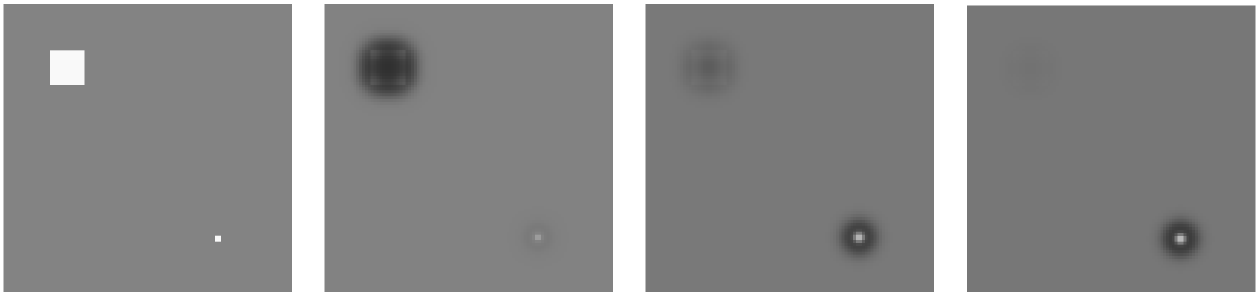

Figure 3: An example of an initial excitation which dies out (on top of the pictures) and one which becomes stable (on bottom of the pictures). The value of r is 12, the excited region of the lower activity is about 4 space units wide. The pictures are snapshots after $t = 0, 1, 3, 10$ time steps from the left to the right.

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[3] For all pictures we have the following colour conventions: a medium gray shows the field in the rest state (about $u = h$), a darker gray indicates refractory regions, and places of a light gray are in the excited state.

3.3 Two-layered DNFs

As mentioned in Section 2, DNFs of two layers support travelling waves. Spiral waves are very stable examples of them and are of great interest in investigating active media (e. g. [16]). If one sets up the field by appropriate initial conditions (as described in Section 2) a spiral wave will emerge (Fig. 5).

Waves in two-dimensional excitable media have some important properties, among them are the curvature and dispersion relation. Without analysing these relations in detail for our model we like to mention that our simulations include both effects, which influence the propagation speed of a wave. The curvature relation states, that convex wave fronts travel slower than plane waves, and concave wave fronts travel faster than plane waves. If the speed of waves increases with an increasing wave length, then the medium includes dispersion. In the first three pictures of Fig. 6 one can see the demonstration of the curvature relation, i. e. the part of the converging waves travels quicker (due to the convex wave front) as the rest of the wave. The last picture of this figure shows the same situation as in the right picture of Fig. 5 but for a slightly changed (increased) parameter w_3 (Equations (4)), which affects the frequency of waves.

4 Simulation results

One question one should ask is: How valueable are all the simulations of the IDEs? Answering this question rises some problems due to the missing analytical results, at least in the two-dimensional case. Of course, it is possible to compare the results of Amari for the one-dimensional DNFs with the results one gets in applying the simulation method to one-dimensional DNFs. In principle, one can say that qualitatively one finds the same types of pattern dynamics as Amari stated. However, a closer look at the quantitative level reveals some differences, some of them should be mentioned here: Because Amari made no assumptions about the boundaries of fields

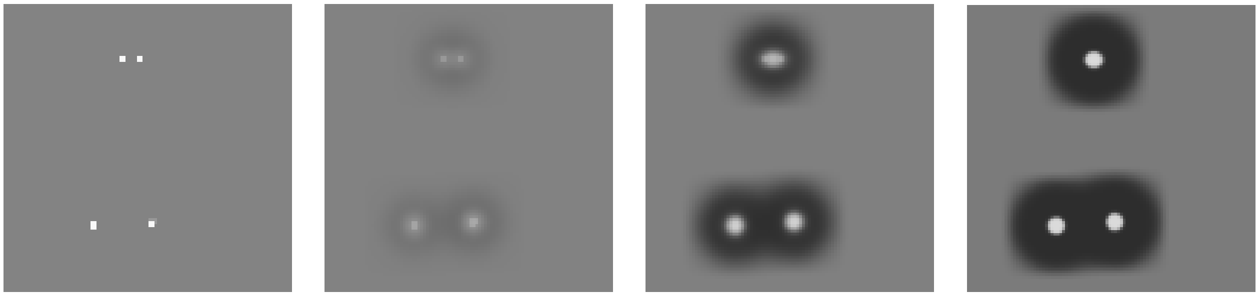

Figure 4: An example of converging (on top of the pictures) and coexisting (on bottom of the pictures) excitations. The value of r is 16, the radius of the positive region of the kernel w is about 7 space units wide. The pictures are snapshots after $t = 0, 1, 3, 33$ time steps.

(he assumed unlimited fields) the simulations show sometimes unexpected patterns at the boundary. Amari determined certain conditions which produce the five types of dynamics. These conditions hold only for continuous fields. In simulations with discrete time and space we only can approximate these conditions. Nevertheless, we could produce the supposed behaviour of all types. A detailed analysis of this approach can be found in [25].

Another way to find out something about the correctness of the simulations is to vary a few crucial parameters and than to compare the results of the simulations. If one can detect differences than the simulations are unstable and sensible to simulation parameters, which would state that the results are of no great interest. As an example one can change the parameter r. From a certain value the enlarging of r should produce no significant difference. For example, in Fig. 1, the crucial part of the one-dimensional mexican hat function is between -7 to $+7$, i. e. the influence of cells which are placed further than 7 space units away can be neglected. For larger r the calculations need more time. Therefore, we have choosen always the smallest possible value for r. In the case of Fig. 1 it would be 7 or 8. Of course, a smaller r would narrow the range of inhibiting connections and the result of the experiments would be not meaningful.

There is one more crucial parameter in the simulations: It is the time constant τ together with the time step Δt in Equation (5). In our simulations we assume $\Delta t = 1$ to be constant. It turned out that the denominator of Equation (5) should be greater than 1 in order to prevent the field to oscillate, i. e. $\tau > 1$. But if one is interested in oscillations one should chose $\tau \leq 1$

The above discussion shows that the CA-like approach is worthwhile to consider. Moreover, the method is of great advantage in studying the influence of different parameters whilst the simulation is running. A direct numerical analysing of DNFs with changing parameters or even with a time dependend input would be on the other hand very hard and time consuming, compared to our very simplyfied method.

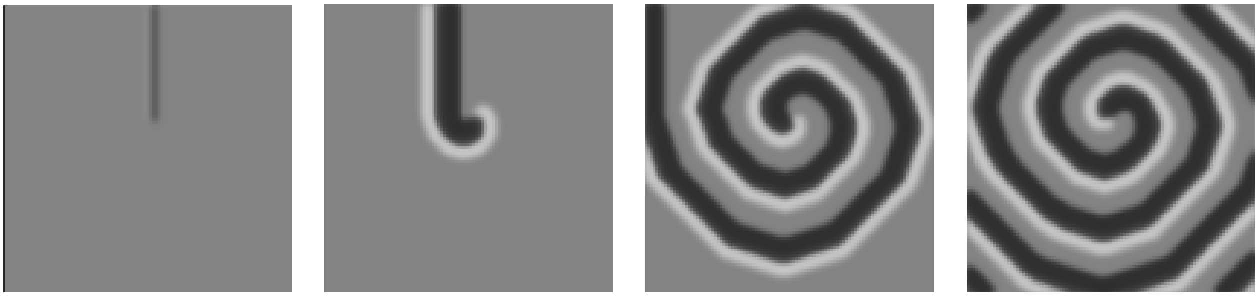

Figure 5: A spiral wave in a two-dimensional DNF with two layers. Only the u_1-layer (in Equations (4)) is shown in the pictures. The u_2-layer shows a similar dynamics with a small time lag. The value of r is 4. The pictures are snapshots after $t = 0, 4, 14, 34$ time units.

5 Applications

One of the neural organizations found in mammalian brains, which are involved in spatio-temporal computations are so-called computational maps (CMs). CMs are a class of neural maps with certain functions. The computational properties of CMs vary with their spatial position. The position of a neuron in the map largely determines (1) which part of the input it receives, (2) how this input is processed, and (3) to what target the result eventually is transfered (see [14] for a discussion). CM discovered so far are mostly involved in processing sensory information and programming of movements ([14]). In motor maps, systematic variations of movement parameters (amplitude and direction) are represented topographically on the neural layer. The computational character of these maps is obvious: the topographically represented movement command must be transformed into spatio-temporal patterns of motoneuron activity, and the centre of activity on the map determines the features of the transformatio.

An example of a CM is the motor map of the mammalian superior colliculus (SC), which major role is to control gaze shifts (saccades), for a review see e. g. [21, 22, 19]. Recording studies of the cat's SC ([17]) showed that during a saccade a hill of activity travels in the motor map from its initial location towards the fixation zone. The instantaneous hill location on the map specifies the remainig motor error. This dynamic can be modelled by using a two-dimensional DNF of one layer. A localiced excitation in that DNF can be thought of as a hill of activity. In order to realize a movement of such a hill we introduce asymmetric place dependend connection functions w. Let $X_1 = X_1(\mathbf{p})$, $X_2 = X_2(\mathbf{p})$ with $\mathbf{p} = (p_1, p_2)$ being a position in space. The connection function (Equation (6)) can be now written as:

$$\begin{aligned} w(x_1, x_2, X_1, X_2) &= a_1 * exp(-(x_1 - X_1)^2/\sigma_1 - (x_2 - X_2)^2/\sigma_1) - \\ & \quad a_2 * exp(-(x_1 - X_1)^2/\sigma_2 - (x_2 - X_2)^2/\sigma_2). \quad (7) \end{aligned}$$

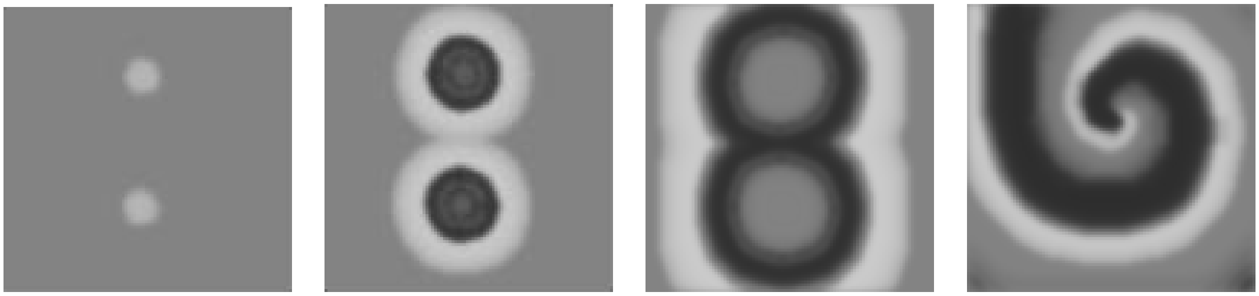

Figure 6: The curvature and dispersion relation. The first three shnapshots show a curvature effect ($t = 0, 5, 11$) and the last picture is a demonstration of the dispersion in the fields. The parameters of the right picture are the same as in Fig. 5 at time $t = 34$ apart from a larger value for w_3. Here again only the u_1-layer is shown.

For $X_1 \neq 0$ and/or $X_2 \neq 0$ the centre of the function (7) is replaced compared to the origin of the coordinate system (Fig. 2). We cannot discuss the model here in detail (for more information see [19]), but the idea should be clear: A smooth variation of X_1 and X_2 in the model of the motor map would ensure, that every activity hill can travel in a predefined direction (here to the region representing the fovea).

So far, the connection function w has been kept fixed in time. The dynamic of excitation patterns will exhibit still more complex behaviour if we introduce a (global) time dependend connection function, i. e. $X_1 = X_1(t)$, $X_2 = X_2(t)$ in Equation (7). This change opens the way to another application, namely to the process of dead reckoning. Dead reckoning, also termed path integration, is a navigation process which allows an animal to update its position (in relation to a point of reference) in an internal representation based on signals generated during locomotion ([3], [4], and [15]). No further visual information which identifies landmarks is needed. The only necessary information is solely generated by movements. By means of this navigation process an animal is able to keep track of its position in the environment in relation to its starting point (or any other point of reference). The necessary information is stored in a geocentric coordinate system, i. e. the position of the animal and of the point of reference is kept in an earth-centered map. Thus, the animal is able to determine the direction of the starting point from its current point and can always move to it without any visual guidance.

Physiological experiments of the navigation system in rats have shown that certain neurons in the hippocampus fire when the rat is placed at a particular position in the environment, regardless of how it is oriented. Cells in the presubiculum fire when the rat's head is oriented in a specific direction regardless of where the rat is ([15]). This situation can be modelled (the model is described in greater detail in [26]) by an two dimensional dynamic neural field $u(\mathbf{x}, t)$ and a dynamic connection function $w(x_1, x_2, X_1, X_2)$. The current position of the animal is indicated in u by a hill of activity (the exact position is the maximum of u, i. e. the top of the activity hill). If the animal moves in a specific direction with a particular velocity this hill will move also in the field in the same direction and a certain distance. These movements are specified by w, whereas w will be updated continuously as the animal moves on. Information of the speed and direction of the animal's movements has to be transformed to X_1 and X_2 in an appropriate manner.

6 Conclusion

The paper has described successful CA-like simulations of two-dimensional DNFs, consisting of one and two layers. The results were compared to the analytical investigations of Amari. It turned out, that the proposed method is of great use, if an analytical solution of the regarded IDE is not available. Further we have argued, that our approach offers some advantages compared to direct numerical calculations, e. g. for the visual following of an ongoing simulation process with time-varying parameters. Particularly, we found the same types of pattern dynamics as Amari found for one-dimensional fields. Additionally, our results indicate that DNFs of two dimensions support target and spiral waves.

In the context of information processing in tissues we used the results to model two spatio-temporal transformation processes found in the mammalian brain. Further experiments, e. g. in application to autonomous mobile robots, have to elaborate and refine the models further. An exhaustive search for different dynamic behaviours in two-dimensional DNFs has not been reported so far, at least not for more than one layer. Thus, simulations like those shown in this paper may help to analyse DNFs with greater complexity as Amari has done.

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