

Title:

Dendritic gates for signal integration with excitability-dependent responsiveness.

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Abstract

The shape and excitability of neuronal dendrites are expected to be responsible for functional characteristics of information processing in the brain. In the present study, we proposed that excitable media with branching patterns mimicked the multi-signal integration of neuronal computation. We initially examined the conditions of the coincidence detection of two inputs as the simplest form of signal integration. We considered a gate with two channels that was bound by a circular joint with uniform excitability and demonstrated that the time window for the coincidence detection was controlled by the geometry and excitability of the gate. The functions of the gate were due to the unique property of the excitation waves, known as the curvature effect. The expanded spatial spread diluted the incoming excitation signals to insufficient levels to sustain wave advancement. Next, we applied dendritic gates that were reminiscent of neuronal dendrites for multi-signal integration. The irregular dendritic patterns were produced by a cellular automaton model of self-organizing pattern formation that adopted the semi-random grid in numerical simulations. We demonstrated that the threshold operation for multiple inputs was conducted by the dendritic pattern. The thresholds varied among gates owing to their irregular patterns, and were adjusted by changing the excitability without changing the gate geometry. The materializable model may provide a novel biomimetic approach for developing fuzzy hardware with adjustable responsiveness.

Keywords:

reaction-diffusion systems; excitability; dendrites.

1. Introduction

The brain processes information and characterizes objects depending on a certain purpose and context. Perceptual sensitivity is highly adjustable so that humans can detect subtle differences among or focus on prominent features of objects. The hallmark of the brain's computational ability, including its variability, is thought to result from the neural networks, which have drawn attention in the arena of novel computer architecture. The contribution of single neurons to computation has long been underestimated (London & Häusser, 2005). In the present study, we shed light on the roles of the dendritic shape and the excitability of the individual neurons and their components in information processing.

Dendritic shapes are ubiquitous in nature. In addition to the neuron, various living systems, such as bacterial colonies, tree branches, leaf veins, blood vessels, lungs, and glandular organs, exhibit dendritic shapes. It has been suggested that dendritic shapes correspond to efficiencies of biological activities, such as transporting substances or transmitting signals. We have aimed to benefit from the design of these dendritic shapes to develop a new computational architecture. As for the realization of dendritic patterns on hardware, Oya and colleagues proposed irregular dendritic pattern formation using a six-layer single-electron circuit (Oya, Motoike, & Asai, 2007). In a similar manner, no neuron presents the identical shape of another neuron. Such diversity likely contributes to the functional variation within the same class of neuron because the cellular shape should affect how the signals are transmitted. We have also aimed to provide a model to examine the contributions of irregular shape and functions among building blocks in computation.

Excitability is defined as the facility to react to and disregard above- and sub-threshold stimuli, respectively, and to produce an all-or-none response. In the neuron, thousands of signals that are received at dendrites are integrated at the origin of the axon, where it is determined whether an electrical excitation, called the action potential, is initiated (Kandel, 2000). Because the neuron has redundant inputs and has thresholds for outputs, we considered that the neuronal process is a form of threshold operation. This process has also been regarded as a coincidence detection mechanism when the effect of time differences between inputs is considered (Agmon-Snir, Carr, & Rinzel, 1998; Jeffress, 1948). To model the threshold operation and coincidence detection on a materializable gate, we focused on the active properties of neuronal dendrites, without accounting for the passive properties of dendrites.

Our idea is based on an interesting phenomenon that occurs during excitation wave propagation and is caused by the curvature effect. It has been observed in chemical (Agladze, Aliev, Yamaguchi, & Yoshikawa, 1996; Tóth, Gáspár, & Showalter, 1994) and biological systems (Cabo et al., 1994) that excitation waves may fail to propagate through a narrow tube toward a broad area. The propagation velocity is formulated as

$$V = (1 - D/K)V_p \quad (1)$$

where D , K , and V_p are the diffusion coefficient, the curvature of the wave, and the velocity of the planer wave, respectively (Zykov, 1988). When the velocity is below the critical value, the wave propagation will stop. This propagation block happens because the diffusive dispersion of the excitation is enhanced at the tube opening, and the outward diffusion

becomes insufficient to sustain the wave advancement. It is interesting to note that the diffusive penetrations from the tube have been observed transiently when a wave diminishes at the tube opening (Tóth, et al., 1994). We have aimed to merge coincidental penetrations to enhance the excitation signals and to revive the wave propagation by applying a particular geometry. This concept is useful in the development of novel schemes for coincidence detection and threshold operation. The curvature effect emerges from the general property of excitation waves; therefore, we have used the simple dynamics of the FitzHugh–Nagumo model to examine our idea using numerical simulations. It has been shown that excitable media have great potential for the implementation of a wide range of computations (Adamatzky, De Lacy Costello, & Asai, 2005; Górecka & Górecki, 2003; Motoike, Yoshikawa, Iguchi, & Nakata, 2001; Steinbock, Kettunen, & Showalter, 1996). However, the operations based on the merged penetrations of the excitation waves are not yet known.

In preceding studies, the computational function of the neuron has been modeled by introducing functions so as to fit to the biological response (Herz, Gollisch, Machens, & Jaeger, 2006). The temporal and spatial summation of neuronal inputs has been considered regarding the addition of EPSPs. In contrast, here we have constructed models of the threshold operation and coincidence detection by displaying the emergent function that arises from the essential property of the excitation waves, where the significance of the medium geometry stands out. In the present study, signal integration was achieved for propagating pulses along dendritic paths.

2. Coincidence detection for two inputs

Coincidence detection is the basis of threshold operation in this study. In this subsection, we describe the analysis of the coincidence detection for two inputs, which is the simplest form of signal integration. We used the FitzHugh–Nagumo model to investigate whether merging coincidental penetration is valid for a wide range of excitation phenomena.

2.1. *Model of excitation wave propagation on a two-armed gate*

The general behavior of the excitation phenomena in biological and chemical systems has been described by the FitzHugh–Nagumo type equations (Fitzhugh, 1961; Nagumo, Arimoto, & Yoshizawa, 1962) as follows,

$$\begin{aligned}\frac{du}{dt} &= f(u,v) = \frac{1}{\tau}(\varepsilon u(u - \alpha)(1 - u) - v) \\ \frac{dv}{dt} &= g(u,v) = u - \gamma v\end{aligned}\tag{2}$$

where u and v are excitation and recovery variables, respectively. τ represents the difference between the excitation and the refractory dynamics time scales. The system excitability depends on the parameter ε , which adjusts the amplitude of the cubic function. α and γ determine the shape of the excitation pulse and the recovery duration, respectively. We set $\alpha = 0.1$ to describe monotonic pulses (Yanagita, 2007) and $\gamma = 0$ for simplicity. Note that Eq. (2) is a scaled version of the FitzHugh–Nagumo model and is essentially the same as the original model equation.

We address the spatiotemporal behavior of excitation wave propagation by introducing a pair of partial differential equations (PDEs),

$$\begin{aligned}\frac{\partial u}{\partial t} &= f(u,v) + D_u \nabla^2 u \\ \frac{\partial v}{\partial t} &= g(u,v) + D_v \nabla^2 v\end{aligned}\tag{3}$$

where ∇^2 is the Laplacian operator, and D_u and D_v are the diffusion coefficients for u and v , respectively. When the excitation wave propagation is compared to the action potential transmission, the excitation variable u corresponds to the membrane potential, which fluctuates due to the ion flux and diffusion. The recovery variable v relates to the switching of the ion channels, and therefore, we assumed that v does not diffuse ($D_v = 0$).

The numerical calculation of the continuous system in Eq. (3) was carried out using the Euler explicit method of integration. The grid size is 256×256 points in a square lattice. The values $\Delta x = \Delta y = 0.026$ and $\Delta t = 0.001$ were chosen so that further decreases in the space and time steps did not markedly improve the accuracy of the calculations for the case when $\tau = 0.005$ and $D_u = 0.0036$.

We designed a two-armed pattern with a circular joint of excitable media in two-dimensional space (Fig. 1A). The joint was roundly widened to enhance a spatial spread so that the curvature effect could be observed. The geometry was determined by three factors: branch width (w), joint radius (r), and the angle between the branches (θ). The branches of equal width w were defined as the input channels, and the output was defined to

be detected at the center of the joint. The branch angle θ was associated with the distance of the input channel connections around the joint circumference for a large r . It was assumed that the excitation waves could only propagate on the excitable media and that excitation would not leak to the unexcitable backgrounds. The no-flux boundary condition was set at the edges and the corners of the field and at the boundary between the excitable media and the unexcitable background. The excitation properties were set to be uniform across the whole structure. At time $t = 0$, $u = 0$ and $v = 0$ were set uniformly. The input stimuli were given transiently by assigning $u = 0.4$ at the end of the input channels.

2.2. Results

The numerical simulation revealed that excitation waves spread over the joint when both of the channels were stimulated simultaneously (Fig. 1B). However, the waves disappeared at the outer side of the joint when only one channel was stimulated (Fig. 1C). This input-output relationship corresponds to the AND operation ($1 \wedge 1 = 1, 1 \wedge 0 = 0$). It should be noted that a time delay between the waves impaired the penetration merge (Fig. 1D). The associated time constraint can be described as the coincidence detection for events that have occurred within a short time window. Because the excitation properties were uniform throughout the gate, this result indicates that the geometry of the excitable media can fulfill the primary role in exerting the operation function.

We tested the condition for coincidence detection and measured the width of the time window (Fig. 2). The wave front curvature became larger as the width w became smaller, enhancing the curvature effect. The joint

radius r also greatly affects the diffusive behavior of the excitation waves because it defines the spatial extent. We tested the width of the time window for the AND operation (the coincidence detection) by changing the time lag between the stimulations of the left and right branches by 100 time steps. The maximum time lag that allowed for coincidence detection is indicated in the gray scale as the width of the time window (Fig. 2A). It was revealed that the ratio w/r relates to, but does not determine, the gate function. As w/r was increased, the width of the time window for the AND operation was enlarged, as shown by the gradation of gray shades between white and black in the plot. When w/r was large enough, one input proved to be sufficient for the output (indicated in white). This function is the OR operation ($1 \vee 0 = 1$). When w/r was small, the excitation waves disappeared at the joint, irrespective of the number of stimulated channels (indicated in black). This result indicates that the gate function depends on the increasing ratio of the spatial spread that enhances the diffusive dispersion.

Fig. 2B shows how the excitability and the distance between the channels affect the gate's function. The distance between the channels increased as θ was increased. The time constraint was delicately controlled by the excitability when θ was small, and the two waves were deeply merged. The increase in the parameter ε , which determined the threshold for excitation, enlarged the time window for the AND operations because high excitability increased the permeability of the excitation waves.

3. Threshold operation for multiple inputs

Coincidence detection can be expanded to the threshold operation by increasing the number of input channels on a computing unit. In this

section, we have used dendritic patterns with small geometrical variations that were generated by a self-organizing algorithm. It has been demonstrated that dendritic patterns reminiscent of neuronal dendrites can be described using reaction-diffusion models (Mimura, Sakaguchi, & Matsushita, 2000; Sugimura, Shimono, Uemura, & Mochizuki, 2007). Among those models, we adopted a cellular automaton (CA) model constructed by Motoike, in which the time and state were discretized and were ultimately suitable for the hardware application (Motoike, 2007). The CA model based on a semi-random grid generates slightly different patterns, which causes variation in the operation results.

3.1. CA model of dendritic pattern formation

Let us give a brief explanation of the CA model. A cellular automaton is the simplest model of spatially distributed processes in which the targeted space is divided into discrete areas, called cells, and the state of each cell is decided using rules at each time step. CA models provide simplified descriptions of systems represented by partial differential equations, reducing computing costs. However, CA models incorporating diffusive behaviors lead to the anisotropy problem in which substances tend to diffuse in orthogonal or parallel directions to the square grids (Markus & Hess, 1990; Takigawa-Imamura & Motoike, 2009). To avoid anisotropy, Motoike adopted Markus's method in which the distances between the cells are randomized by assigning the i th- j th cell to a position of $(\hat{i}, \hat{j})$, where $\hat{i}$ and $\hat{j}$ take real numbers in the interval $(i, i+1)$ and $(j, j+1)$, respectively (Markus & Hess, 1990; Motoike, 2007).

The rules of the CA model are based on a pattern formation model of bacterial colonies with a reaction-diffusion system (Mimura, et al., 2000; Motoike, 2007). It was assumed that *active paths* (a) diffuse and transform to *stable paths* (s) at rates that depend on the number of *active paths* and the amount of *nutrients* (n) in their surroundings. These interactions are represented by the following rules,

$$a^{ij}(t) = 0 \text{ and } n^{ij}(t) \geq n_c \text{ and } E_a^{ij}(t) \geq a_c \Rightarrow a^{ij}(t+1) = 1 \quad (4)$$

$$a^{ij}(t) = 1 \text{ and } (n^{ij}(t) < n_c \text{ or } E_a^{ij}(t) < a_c) \Rightarrow a^{ij}(t+1) = 0, s^{ij}(t+1) = 1 \quad (5)$$

$$n^{ij}(t+1) = \max \left\{ \frac{1}{\# N_n^{ij}(t)} \sum_{\sqrt{(\hat{k}-\hat{i})^2 + (\hat{l}-\hat{j})^2} \leq R_n} n^{kl}(t) - a^{ij}(t) \cdot c, 0 \right\} \quad (6)$$

where $a^{ij}(t)$ and $s^{ij}(t)$ take the binary state (0,1), to indicate whether the i th- j th cell is an *active* and *stable path* at time step t , respectively. $n^{ij}(t)$ indicates the nutrient concentration and is represented by an integer that ranges from zero to an initial nutrient concentration $n(0)$. The diffusion of active paths and nutrients was described by introducing R_a and R_n , which are the radii that define the neighboring cells of the i th- j th cell. $N_n^{ij}(t)$ and $\# N_n^{ij}(t)$ designate a set and the number of the neighboring cells, respectively. $E_a^{ij}(t)$ is the number of active paths in its neighborhood defined by R_a . The constants a_c and n_c are the thresholds of $E_a^{ij}(t)$ and $n^{ij}(t)$ for bacterial proliferation, respectively. Eq. (6) describes the consumption and diffusion of the nutrients by averaging the amount of nutrients within the neighboring cells. Finally, c is the nutrient consumption rate.

We calculated the rule in Eqs. (4)–(6) in a square lattice of lateral size $L = 200$, with a unit cell length $d = 1$. Each cell was initially assigned to a position of $(\hat{i}, \hat{j}) = (i + \eta_i^{ij}, j + \eta_j^{ij})$, with η representing different and uncorrelated random values that were uniformly distributed in the interval (0,1). The initial values for nutrient concentration $n(0)$, for the indication of the active path $a^{ij}(0) = 0$, and for the indication of the stable path $s^{ij}(0) = 0$ were given uniformly. The pattern formation was initiated by casting a *seed*, a cluster of active paths, in the center of the field. The radius of the *seed* was set at $r = 20$ which was sufficiently large to cause conditional propagation. The calculation was iterated until no change was observed in the pattern.

Figs. 3A and B show examples of the result of the CA model that led to a dendritic pattern of stable paths. The dendritic pattern almost evenly covered the field by radial stretches and distal branching. The branches rarely reached the edge of the field due to the nutrition shortage that occurred at the late stage of the branch elongation process. The detailed geometry varied with changes in the cell's positioning, while the other parameter values were kept constant (Fig. 3C). Because the behavior of the excitation wave propagation greatly depended on the geometry of the excitable media, it was expected that small variations in the geometry would result in the irregular operation results.

3.2. Coincidence detection on the dendritic gate

In preparing to examine the threshold operation, we confirmed that coincidence detection could be conducted on the dendritic patterns, as was

possible in the two-armed gate. It was assumed that the dendritic pattern had excitability, while the background did not. Fig. 4 shows the behavior of the excitation propagation when a few branches were stimulated simultaneously at the upper edge of the pattern. Note that the pattern formation was achieved using the discrete CA model, while the behavior of the excitation waves was calculated in the continuous system. When only one branch was stimulated, the excitation waves failed to propagate through the joint (Figs. 4A–C). In many cases, waves turned into next branches and moved upward, though such excursions do not affect the output event defined here. It is suggested that excitation signals from a branch are enough to deliver waves to another branch but not to the joint, which is much wider than a branch. Such behavior is not a result of reflection, but rather attained by the incursion of excitation signals into adjoining excitable paths.

When excitation waves from the different branches simultaneously penetrated the joint, the waves merged and the excitation waves were diffused over the joint (Fig. 4D). Two excitation penetrations with a time lag, however, failed to merge (Fig. 4E). The behavior of the excitation waves corresponded to the coincidence detection. In the dendritic gate, the time lag resulted from the differing path lengths that were longer at the corner and shorter in the middle of the field. In addition, variation in the branch shapes affected the operation results. A wide root of a dendritic tree works as the OR operator (Supplemental Movie S2F), which corresponds to the case when w/r is large. In contrast, waves may disappear on very narrow branches (Supplemental Movie S2G). These behaviors increased the functional variations as a result of the geometrical variations.

3.3. *Threshold operation on the dendritic gates*

In the previous subsection, we observed that a dendritic gate's output depends on the spatial arrangement of the input signals. In this subsection, we have examined how the gate responds to inputs of various densities. It was assumed that a dendritic gate has many input units and emits one output, which is in agreement with the fact that a neuron fires according to the results of the integration of many stimuli. Input sequences of 20 bits were given at the upper edge of the gate, and the output was defined to be detected at the joint center (Fig. 5A). The input sequence was randomly decided irrespective of the gate pattern; therefore, the input signals that were given on unexcitable backgrounds were invalid.

Fig. 5B shows the summary of the responses of 100 different dendritic gates that were generated from various cell position assignments. We defined the response rate as the occurrence of the output events to the trials that 10 different input sequences of the same signal density are given to a gate. The mean response rate was calculated from the response rates of 100 individual gates that were obtained using identical parameter set with different $(\hat{i}, \hat{j})$ distributions. In Fig. 5B, the mean response rates increased as the input signal densities increased, indicating that the gates underwent the threshold operation. It was also confirmed that the excitability ε controlled the responsiveness of the gates without changing the output pattern, which was also the case for the two-armed gates. In the case of $\varepsilon = 2.25$, the response rate correlated well with the input signal density, indicating that the response rate can be considered an indicator of the input signal density. Fig. 5C shows that the thresholds of the input density for

responses were highly varied among the gates, indicating that the variation in the shapes caused the functional variation.

3.4. Information compression on the dendritic gate queue

In view of the application of the functional characteristics of dendritic gates, we have used the dendritic gates to compress a data sequence (Fig. 6). We designed a queue of excitable dendritic gates by casting many seeds in a long field. Fig. 6A shows an example in which many dendritic patterns that grew in a given space showed almost complete coverage, but clear gaps remained between the units. We used these computing queues to process a binary data sequence (Fig. 6B) so that each gate received 10–40 bits of information via the upper edges of the gates. It was demonstrated that the dendritic units at the dense/sparse signal areas output with high/low probabilities (Fig. 6C), resulting in information compression. The gain was controlled by excitability (Fig. 6D). The compression rate was determined by the number of gates (Figs. 6C–E).

The compressed results were inaccurate due to the diverse responsiveness of the gates. This shortcoming is inextricably associated with an advantage in the conservation of the information of the input density. We examined outcomes of the gate queue when it received input signals (Fig. 7A) from the regularly distributed sequence. The queue emitted an output sequence with a density similar to the total input density (Fig. 7B). These results are equivalent to those in Fig. 5B. In contrast, in a queue that consisted of identical gates, the output densities became either 0 or 1, resulting in a loss of information of the total input density (Fig. 7C).

4. Discussion

Neural networks may utilize feedback to regulate their excitability and to obtain an appropriate gain for information processing. In image processing, neuronal responses in the primary visual cortex are facilitated or suppressed, depending on the contrast of the stripe pattern in focus (Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998; Schwabe, Ichida, Shushruth, Mangapathy, & Angelucci, 2010). The adjustable threshold operation in our model seems to be involved in the mechanism of flexible computation in the brain. The perceptive recognition in living organisms contains errors and ambiguities that are affected by their physiological status. In order to overcome the inaccuracy of the operation in the nervous system, real neural networks would have redundant circuits for processing a piece of information. The information compression in Figs. 6 and 7 are consistent with the fuzzy and robust operations carried out by neurons.

Considering that the curvature effect depends on the convex wave front and the wave permeability (Tóth, et al., 1994), the functional effects of the geometry and the excitability suggest that the operation on the two-armed gate was due to the curvature effect. The curvature effect occurs as a result of a general property of the excitation waves, and it will also be observed in other excitation models including Hodgkin–Huxley dynamics. The purpose of our model was not to explore the mechanism of neuronal computation. We have focused, rather, on how the signal integration mechanism of our model might associate with that of the neuron. An investigation of the contribution of neuronal morphology and the excitability to computation will be the focus of our next study.

Yanagita has investigated excitation propagation in a trifurcated structure that included three mathematical cables of zero diameters, which was driven by the transmission of an action potential (Yanagita, 2007). It was shown in this previous report that a propagation block at a branch point can be recovered by an interaction between the stimulations from different branches. The result in this generalized model was consistent with the coincidence detection in our two-armed model in two-dimensional space. By introducing the circular joint, our study highlighted the contribution of the medium geometry to the curvature effect and to the penetration merge. In contrast to our study, which used monotonic wake pulses, oscillating wake pulses were used in the Yanagita model, with a focus on the interaction between a pair of pulses.

Since Turing established the theoretical concept of diffusion-driven pattern formation, the reaction-diffusion system has been used to explain many static and spatiotemporal patterns of self-organization (Cross & Greenside, 2009). In the present study, we have adopted two distinct dynamics of reaction-diffusion systems: a dendritic pattern formation in a cellular automaton framework and excitation waves in a continuous system. The mutual promotion of these dynamics was examined to develop a unique system that generated dynamic path pattern reconfiguration in response to input (Motoike & Takigawa-Imamura, 2010; Takigawa-Imamura & Motoike, 2009). In contrast, in the present study, we have examined behaviors of signal propagation on static path geometries and have aimed to apply these dendritic patterns to computing devices.

It is expected that dendritic gates have the potential to execute complicated computations. The subtraction between output sequences that was obtained for different excitabilities in Fig. 6D results in contour

definition of the corresponding input sequence. The refractory state that blocks excitation wave propagation may be utilized to achieve the subtraction. As for the temporal integration of input signals, it is also possible to observe an output emission that depends on the velocity of a moving object with respect to the input sequence. In addition, it would be of interest to consider the interaction between gates by choosing appropriate parameter values so that the dendritic units would interact with each other.

Reaction-diffusion processes have been investigated in the context of unconventional computing devices over the last two decades (Adamatzky, et al., 2005). The Belousov–Zhabotinsky reaction will be able to confirm our ideas, although such chemical systems are too slow and fragile to be applied for practical computation. Is it possible, then, to implement the proposed function of the dendritic gates for hardware? If so, this technology might provide a basis for new artificial intelligence that is composed of building blocks that exhibit varying responses. Single-electron circuits that perform dendritic pattern formation, proposed by Oya and colleagues, are logically possible. However, these circuits would be difficult to realize with current technology (Oya, et al., 2007). Alternatively, it was suggested that viscous fingering at an extraordinarily high viscosity rate in silica glass could replicate the nanoscale dendritic grooves that are observed in basalt rocks (French & Muehlenbachs, 2009). At present, these ideas relate to the materialization of dendritic patterns. Next, the focus must shift to the development of excitable media for computing devices. In spite of the technical difficulties in implementation, we believe that the novel idea of signal processing on dendritic patterned excitable media is an important topic to study, exploiting the significance of multi-signal

integration and the varying responses of the building blocks that are involved in computation.

5. Conclusion

Inspired by the shape and function of the neuron, we have investigated what kind of information processing can be conducted on excitable media with dendritic shapes. We have employed self-organized pattern formation dynamics to produce irregular dendritic patterns, and have showed that the dendritic gates conduct varying threshold operations for multiple inputs. The threshold operation of the dendritic gate was realized by expanding the coincidence detection on the two-armed gate, which is a novel idea in computing devices of excitable media. We have suggested that the response rate could encode the input signal density in a collection of gates with varying responsiveness. The most interesting feature of the two-armed gates and the dendritic gates was the adjustability of their functions by changing their excitability without changing their geometries. The gate geometries and the excitability are responsible for the functional characteristics of the gates, which is also true of the networks in the brain.

Acknowledgments

We are deeply grateful to Associate Professor Tetsuya Asai for the helpful discussions and comments. We also thank Professor Konstantin Agladze and Professor Kenichi Yoshikawa for their guidance and support. This work was supported by JST PRESTO program.

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Figure Legends

Fig. 1

The coincidence detector of excitable media. **(A)** Example of the two-armed pattern with a circular joint. White and light gray regions indicate excitable media and unexcitable backgrounds, respectively. Black lines denote branch width (w) and joint radius (r). The arrow indicates the branch angle (θ). Values for the parameters were taken to be $w = 7$, $r = 18$, $\theta = \pi/3$. **(B–D)** The wave propagation on the geometry shown in **(A)**. Snapshots were cut out around the joint and were sampled every 500 time steps. Stimulations were applied to the channel region located 123~133-cell distances from the center of the joint. The gray shades on the excitable path indicate the u value, with black indicating the highest u value. The system excitability was set to be $\varepsilon = 2.0$. The corresponding movie is provided as Supplemental Movie S1. **(B)** Both channels were stimulated at once. The penetrations merged at the entrance to the joint. The excitation wave was sustained and spread over the joint. **(C)** The left channel was stimulated. The excitation wave disappeared at the joint. **(D)** The right channel was stimulated at 500 time steps after the left channel was stimulated. As shown in this figure, penetrations with a time delay did not successfully merge.

Fig. 2

The excitability and geometry of the excitable media determined the gate functions. The maximum time lag that allowed for the coincidence

detection is indicated in the gray scale, except for the cases when the waves never propagated through the joint (indicated by black) and when a single stimulation was sufficient to sustain the wave propagation (corresponding to the OR operation, indicated by white). **(A)** The w and r values were changed in the cases of $\varepsilon = 2.0$ and $\theta = \pi/3$. **(B)** The ε and θ values were changed in the cases of $w = 5$ and $r = 12$.

Fig. 3

Examples of the dendritic pattern formation. **(A, B)** The stable paths produced from the cellular automaton model are indicated by white on black background. These patterns shown were obtained using different $(\hat{i}, \hat{j})$ distributions with the same parameter set $n(0) = 50$, $n_c = 40$, $a_c = 1$, $c = 10$, and $R_a = 2$. The seed size was set at $r = 20$. Branches often fuse to other branches at their root under this condition. **(C)** An overlap of the results from (A) and (B). Black, gray, and white indicate the overlapping backgrounds, non-overlapping backgrounds, and overlapping paths, respectively.

Fig. 4

Behaviors of excitation waves on the dendritic pattern shown in Fig. 3A. The dendritic pattern (white) and background (light gray) were defined to have and not to have excitability, respectively. The gray shades on the excitable media indicate the u values, with black indicating the highest u value. The snapshots were sampled every 600 time steps. The corresponding movies are supplied as Supplemental Movies S2A–E. **(A–C)**

When a branch was stimulated, the wave did not spread over the joint, but rather traveled backward through the adjoining branch. **(D)** The branches stimulated in **(A)** and **(B)** were done so simultaneously, and the merged penetration revived the wave propagation in the joint. **(E)** The branches stimulated in **(A)** and **(C)** were also done so simultaneously. The difference in the branch lengths caused a time lag, which resulted in the failure of the penetration merge.

Fig. 5

The gate response. **(A)** The input area was defined as a 10-cell height region at the upper edge, which was divided into 20 units. The output was defined to be detected at the center of the gate. Each dendritic pattern was generated using the parameter set in Fig. 3, but with various $(\hat{i}, \hat{j})$ distributions. **(B)** The excitability–dependency of the mean response rate. The number of the output events to 10 different input sequences of the same signal density was counted for 100 individual gates, and the mean response rate was calculated. **(C)** Differences in the responses among gates. The box-whisker plot shows the response rates for the case when $\varepsilon = 2.25$. The horizontal line indicates the median while the box covers the 25–75% percentiles. The maximum length of each whisker is 1.5 times the interquartile range. The asterisk indicates the mean.

Fig. 6

Information compression of a binary data sequence on the dendritic gate queues. **(A)** An example of the dendritic gate queue. The queue was

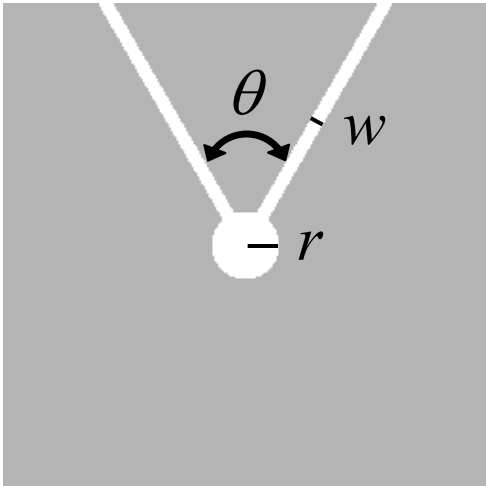
generated by placing 20 seeds in a 2000×200 field at the regular interval. Note that each gate varies slightly in shape. **(B)** An input sequence of 400 bits. Stimulating signals (black regions) were applied on the top of the queue. **(C)** The output sequence and the excitation wave behaviors when the input sequence in **(B)** was processed on a queue that consisted of 10 dendritic gates for the case when $\varepsilon = 2.25$. The snapshots were sampled every 500 time steps. The corresponding movie is supplied as Supplemental Movie S3. **(D)** The excitability-dependency of the output sequence from a 20-gate queue. **(E)** The output sequence from a 40-gate queue for the case when $\varepsilon = 2.25$.

Fig. 7

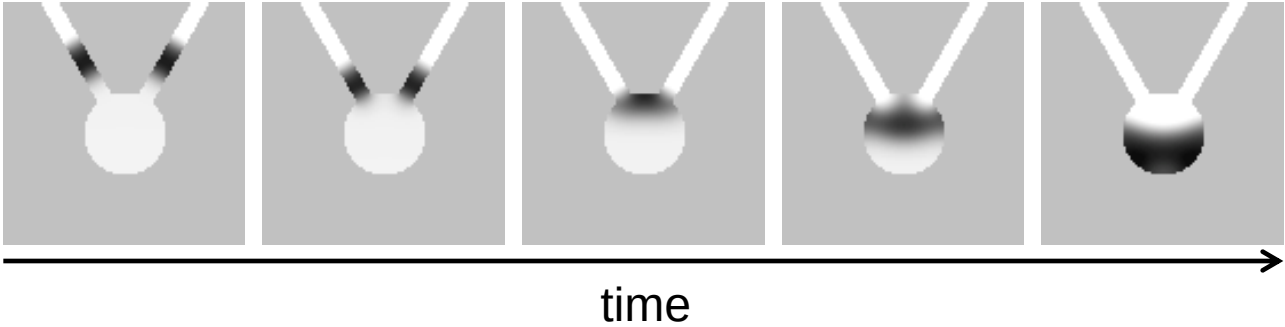
Information compression of regularly distributed input sequences. A 40-gate queue and an 800-bit input sequence were used with $\varepsilon = 2.25$ for both cases. **(A)** Input sequences of various input densities. **(B)** Output sequences from an irregular dendritic gate queue. **(C)** Output sequences from a queue that consisted of identical dendritic gates.

Fig. 1

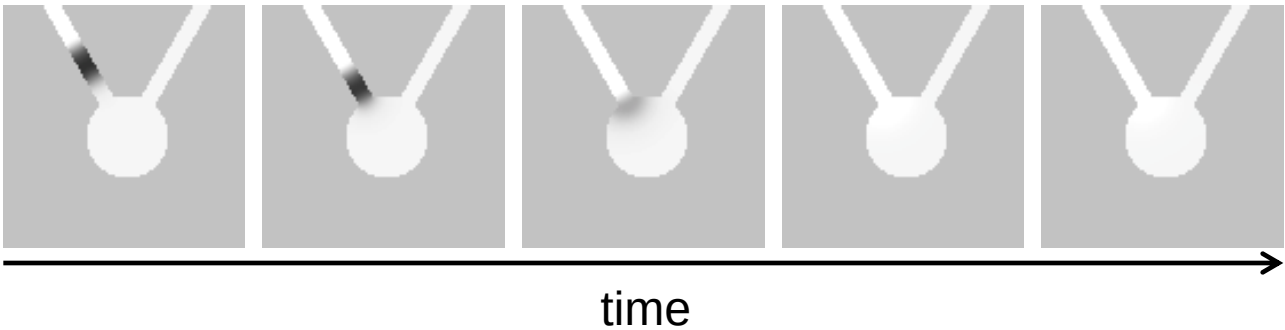
A



B



C



D

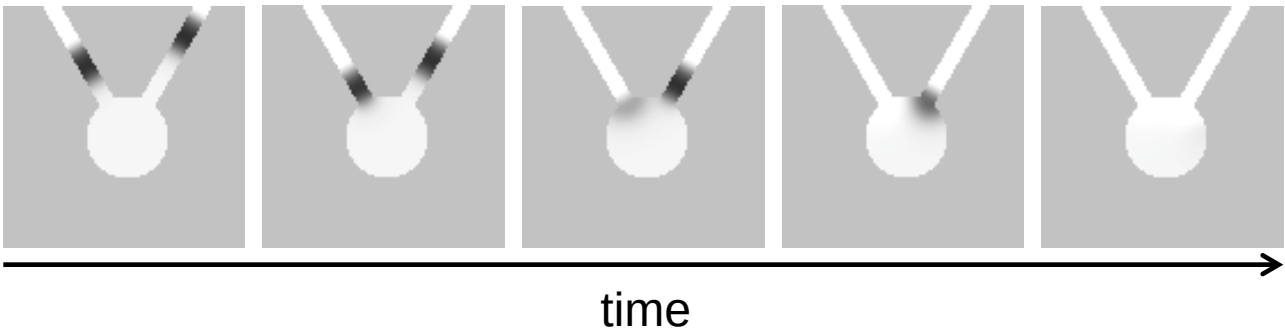
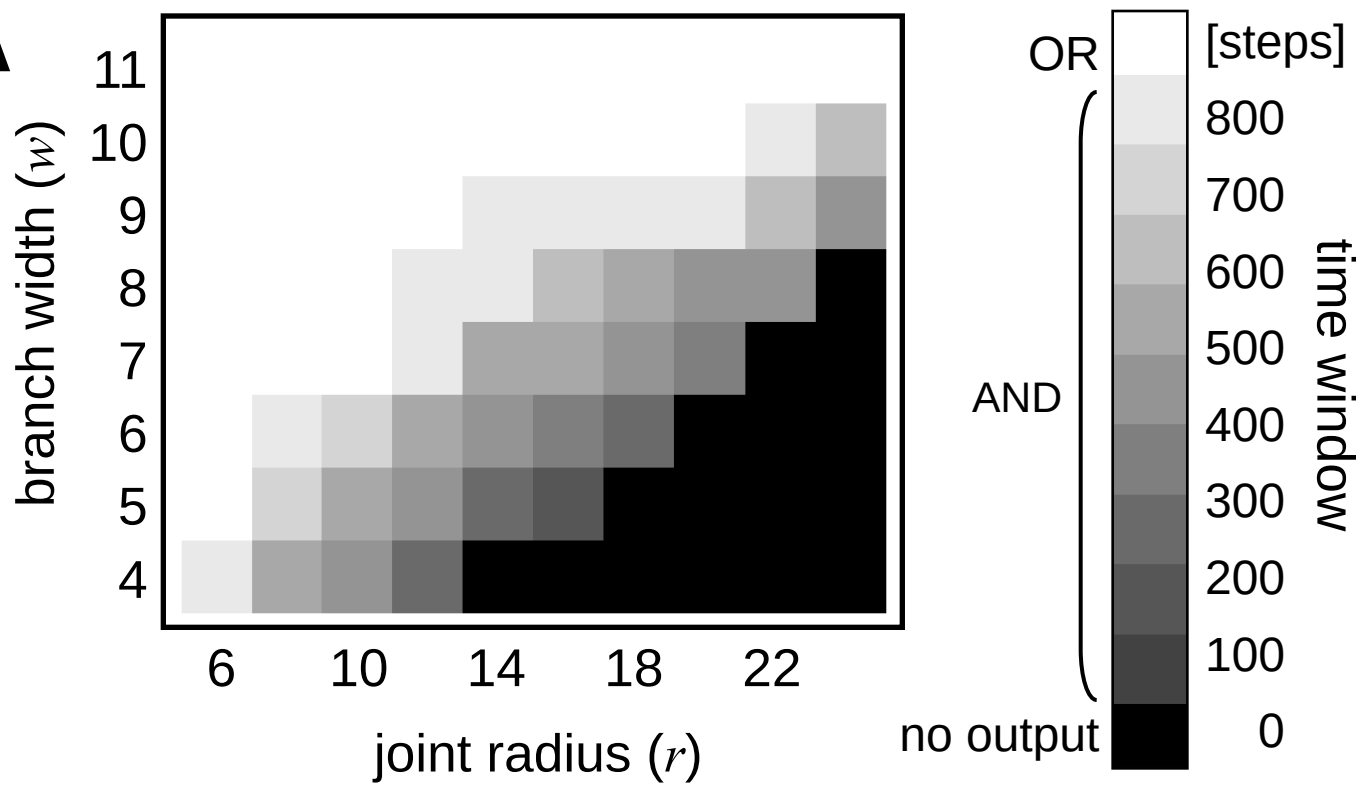


Fig. 2

A



B

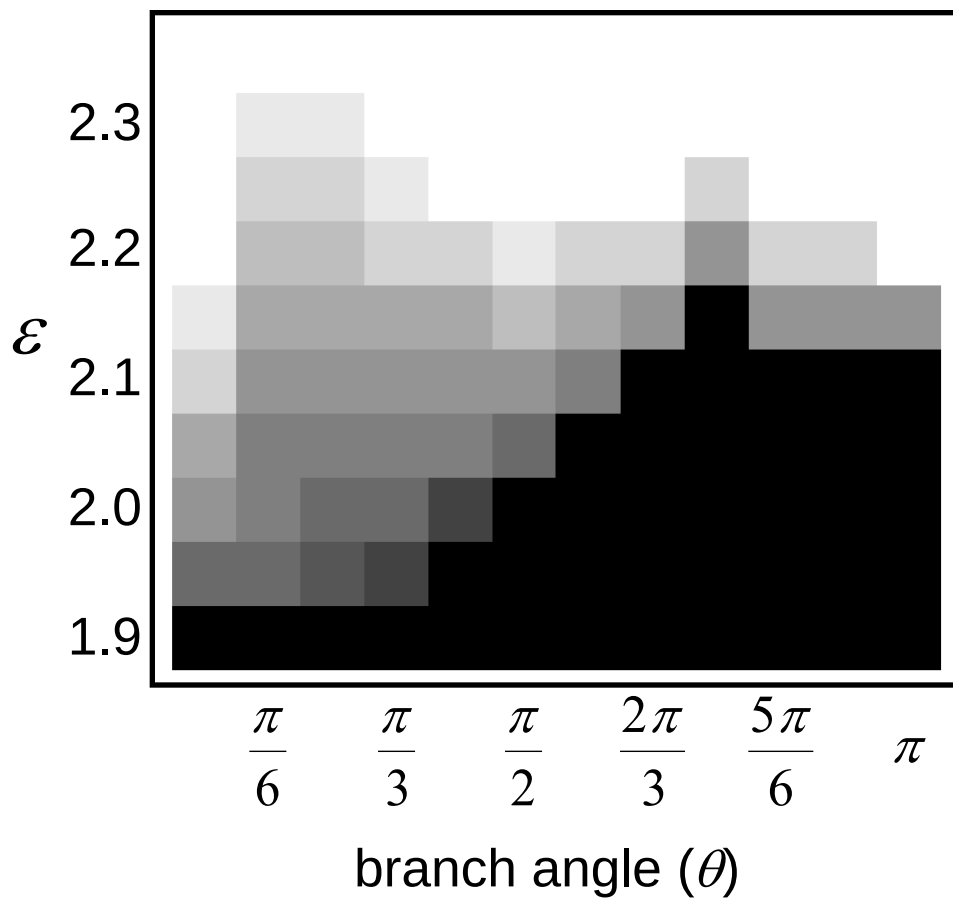
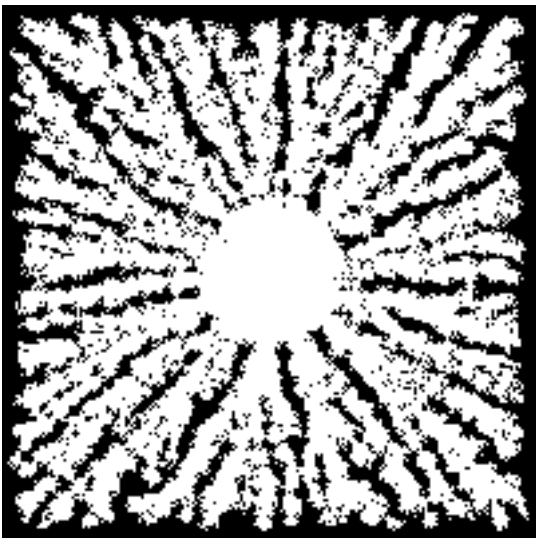
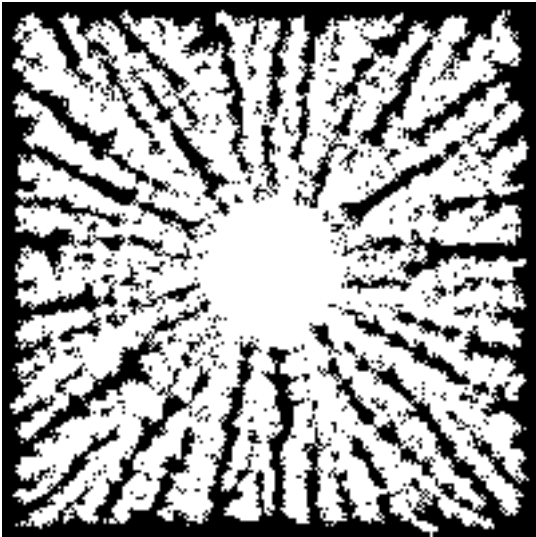


Fig. 3

A



B



C

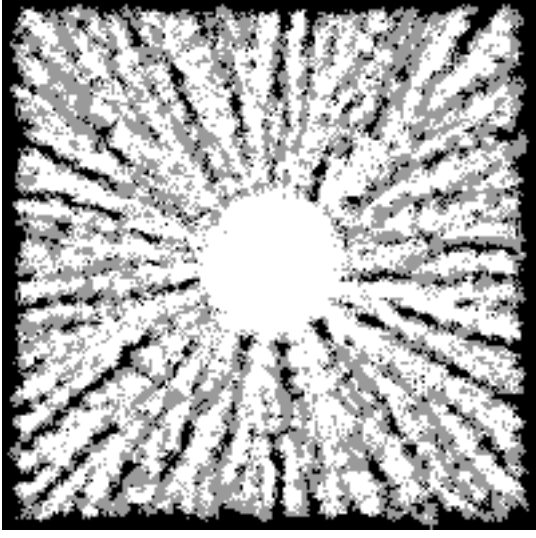
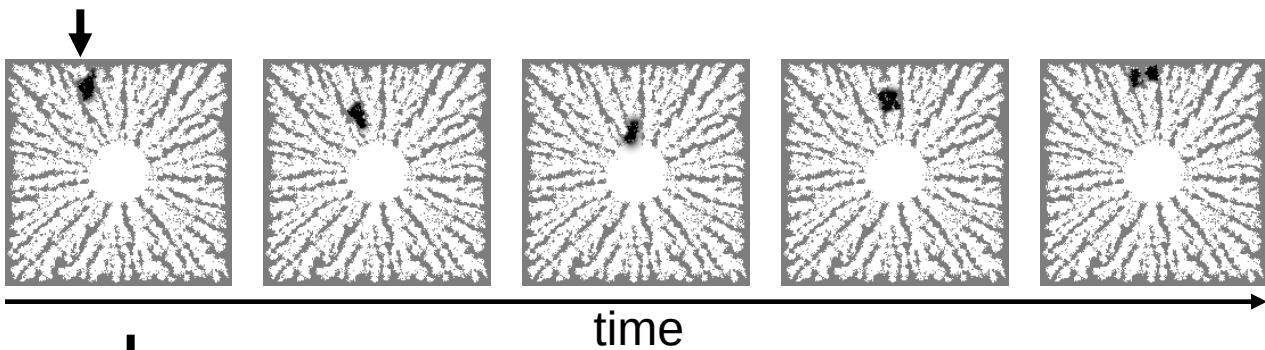
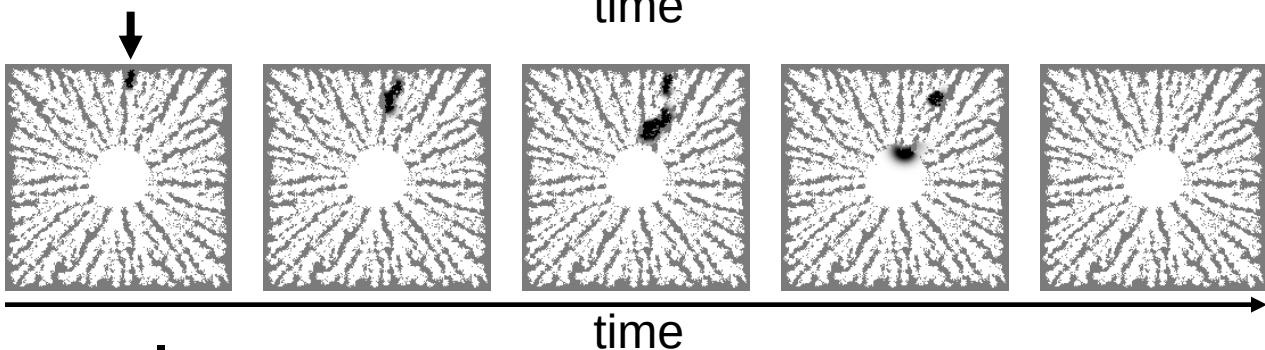


Fig. 4

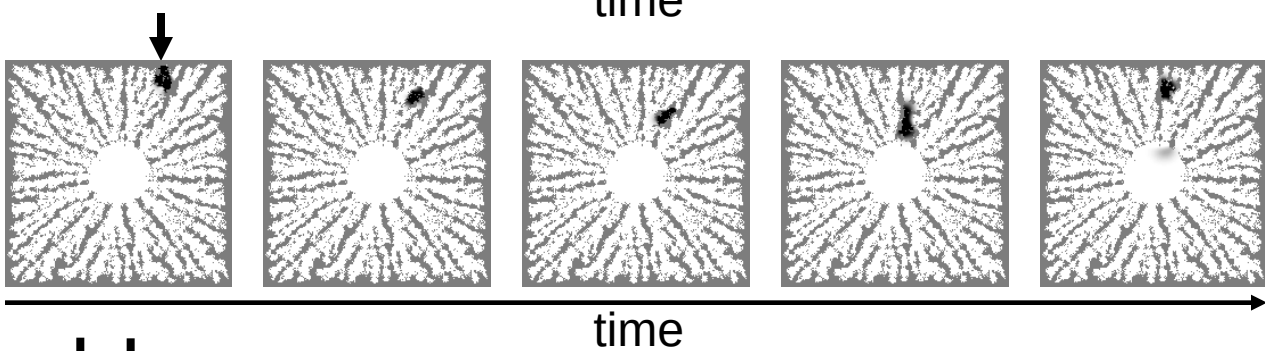
A



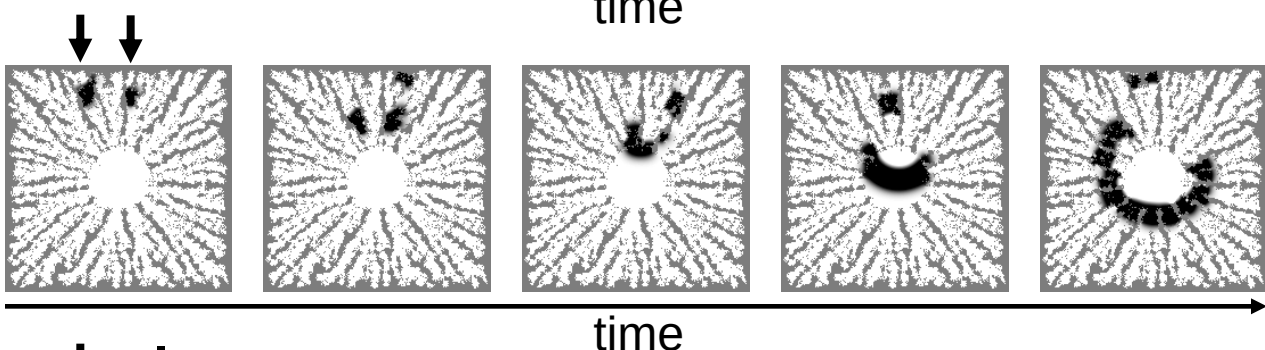
B



C



D



E

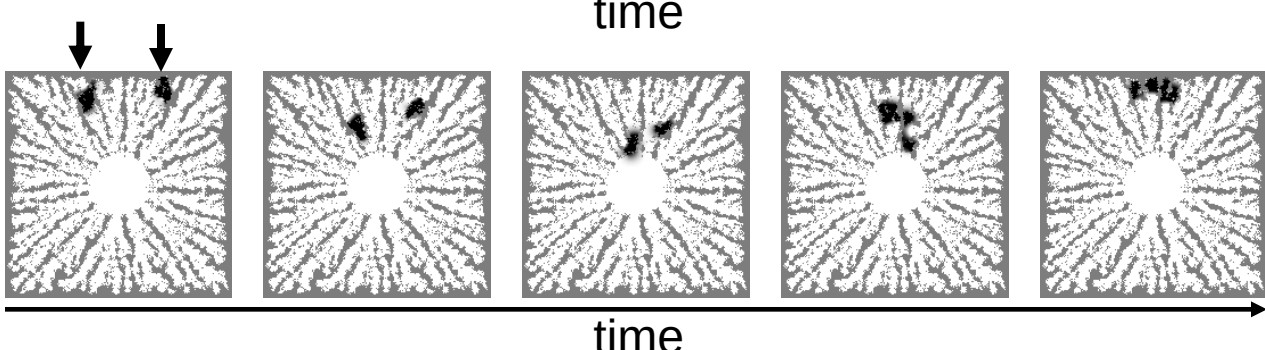


Fig. 5

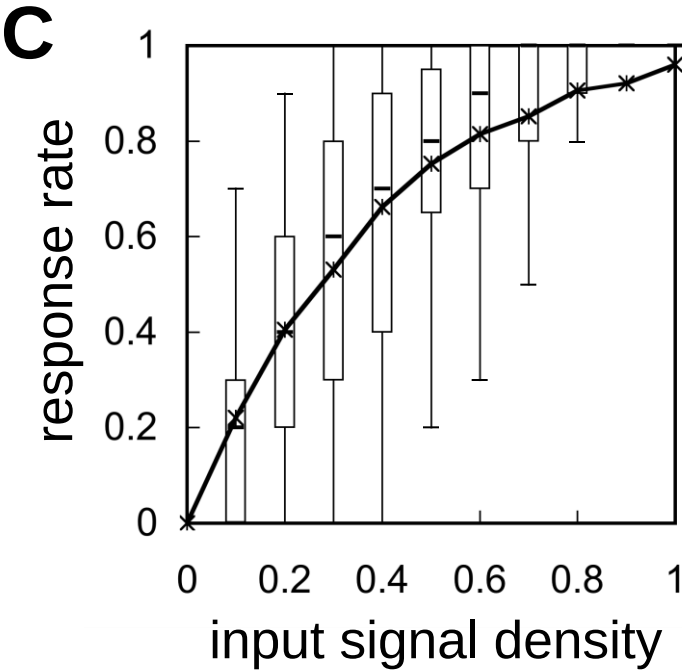
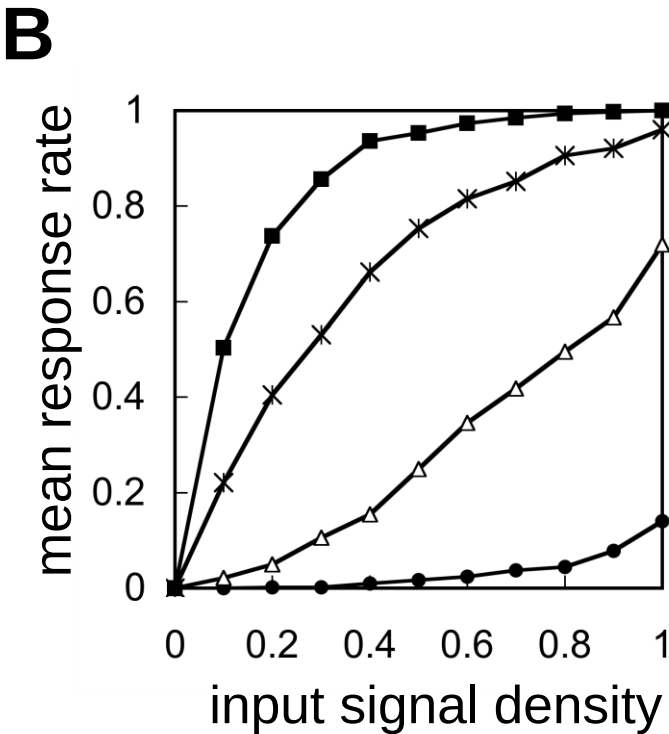
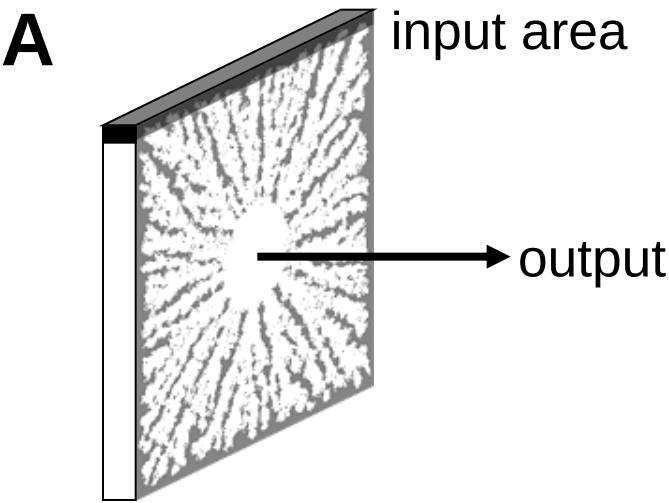
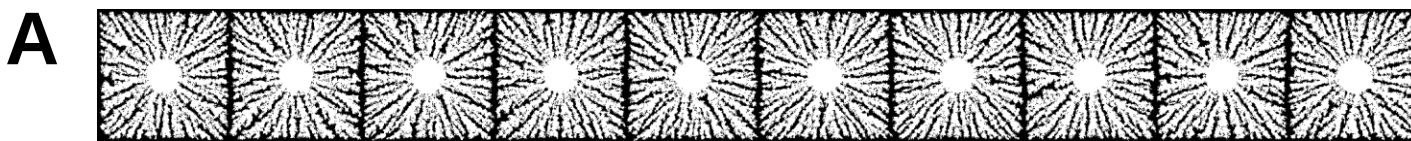
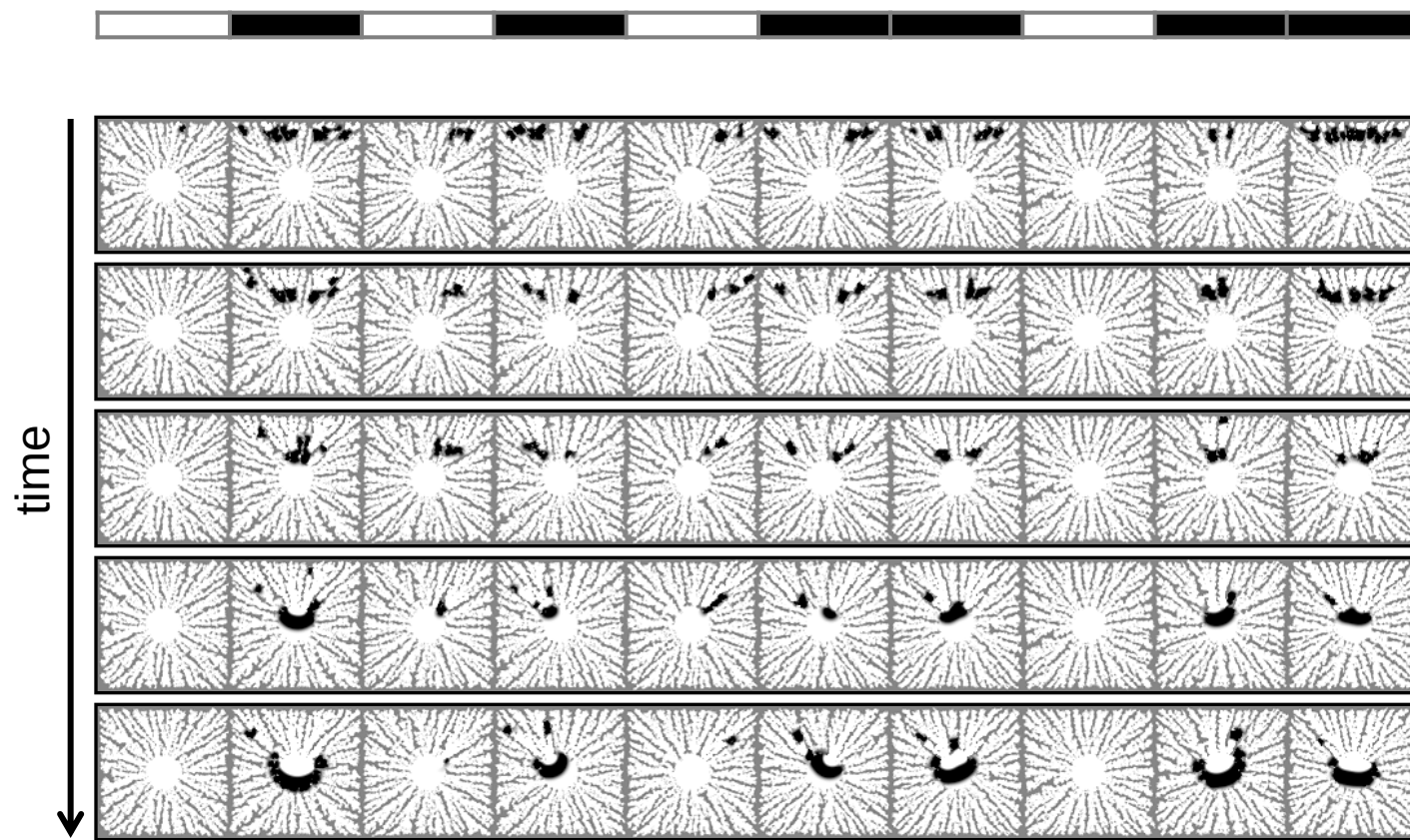


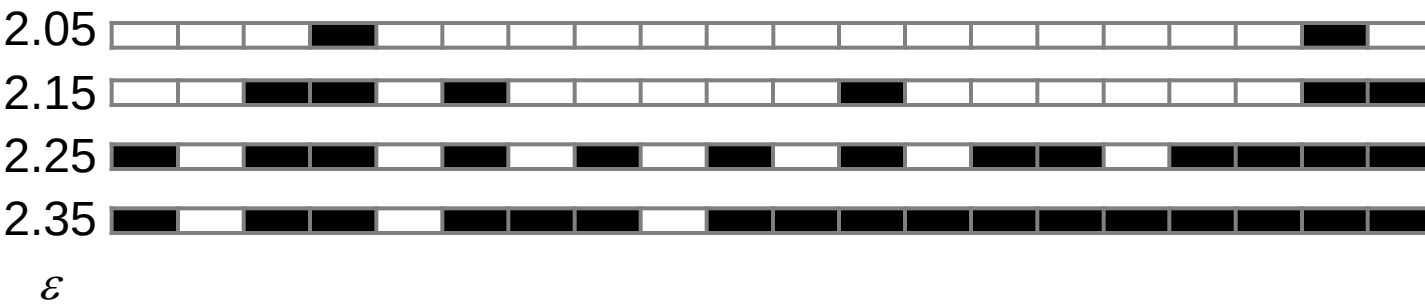
Fig. 6



C 40 bits/gate



D 20 bits/gate

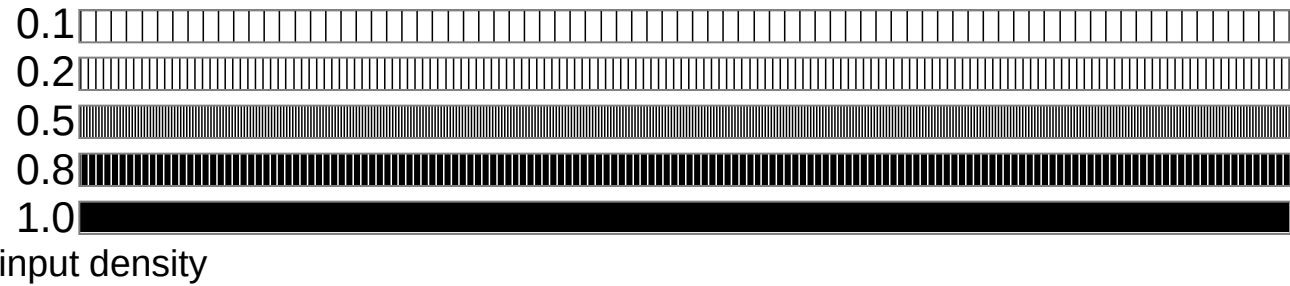


E 10 bits/gate

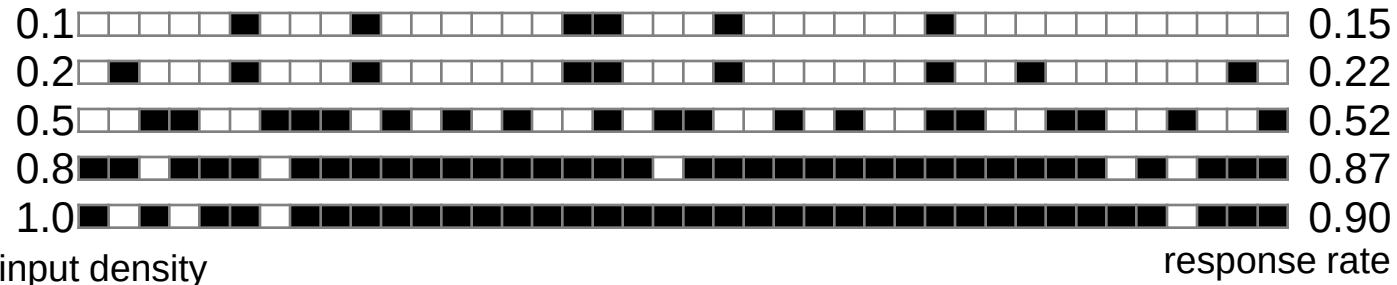


Fig. 7

A



B



C

