# Weierstraß-Institut

## für Angewandte Analysis und Stochastik

### Leibniz-Institut im Forschungsverbund Berlin e. V.

# Detection and storage of multivariate temporal sequences by spiking pattern reverberators

Leonhard Lücken ,  Serhiy Yanchuk

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Weierstrass Institute
Mohrenstr. 39
10117 Berlin
Germany
E-Mail: leonhard.luecken@wias-berlin.de
         serhiy.yanchuk@wias-berlin.de

**Abstract**

We consider networks of spiking coincidence detectors in continuous time. A single detector is a finite state machine that emits a pulsatile signal whenever the number incoming inputs exceeds a threshold within a time window of some tolerance width. Such finite state models are well-suited for hardware implementations of neural networks, as on integrated circuits (IC) or field programmable arrays (FPGAs) but they also reflect the natural capability of many neurons to act as coincidence detectors.

We pay special attention to a recurrent coupling structure, where the delays are tuned to a specific pattern. Applying this pattern as an external input leads to a self-sustained reverberation of the encoded pattern if the tuning is chosen correctly.

In terms of the coupling structure, the tolerance and the refractory time of the individual coincidence detectors, we determine conditions for the uniqueness of the sustained activity, i.e., for the funcionality of the network as an unambiguous pattern detector. We also present numerical experiments, where the functionality of the proposed pattern detector is demonstrated replacing the simplistic finite state models by more realistic Hodgkin-Huxley neurons and we consider the possibility of implementing several pattern detectors using a set of shared coincidence detectors. We propose that inhibitory connections may aid to increase the precision of the pattern discrimination.

# 1 Introduction

During the recent years an increasing interest was directed towards the possibility of neural information coding with time-differences between spikes of different neurons [1–7]. For instance, sensory stimuli of various types were shown to be encoded and processed as such multivariate sequences of spikes [8–17]. Furthermore, also primarily cognitive processes, related to mnemonic or associative tasks, are widely believed to be manifested in precisely timed patterns of spike-times [6, 11, 14, 18–21].

As a possible origin of the observed phenomena, Abeles [22] proposed the activity of synfire chains. These consist of feedforward connected layers of neurons through which a wave of excitation can propagate from layer to layer where at each stage the neurons in the same pool fire synchronously. A specific stimulus activates a specific synfire chain that is guided from one layer to the next and thereby creates patterns of the observed type.

However, models of synfire chains do not account for heterogeneous axonal, synaptic and dendritic delays, which do exist within the brain [12, 23–26]. If non-identical delays are included there is still a possibility that an excitation is propagated through the network, if at each participating neuron a sufficient number of inputs converges within a sufficiently narrow time window. For each neuron this coincidence of inputs depends on the temporal signature of the activity of

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its predecessors such that the activation of the entire chain must appear as a precise orchestration of coincidences. The emerging propagating structures were introduced as "synfire braids" by Bienenstock [27] and later studied under the term "polychronous groups" (PGs) by Izhikevich [28]. It was shown that they arise naturally in sufficiently complex random networks constructed in physiologically plausible parameter ranges [28–30]. There are two major implications of heterogeneous delays. Firstly, the neurons which participate in the propagation do not necessarily fire synchronously and in a clocked manner, i.e. in well-defined layers. The obsererved firing-sequence is now a general multivariate pattern. Secondly, the systems storage capacity in form of the number of distinct responses to inputs is believed to be potentiated [28]. An appealing feature of the "web" of PGs is their complex interleaving: One neuron can be part of different but overlapping groups – even the same ensemble of neurons may constitute different PGs.

The theoretical properties and computational capabilities of PG networks received an increasing interest in the past years [28, 31–33]. The number of PGs of a network, which reflects the number of information processing pathways was studied numerically [28, 30, 34–37] but it is difficult to obtain a theoretical estimate and none is available up to date, as far as we know. Methods for reservoir computing have been developed which exploit the dynamical formation of PGs by spike-timing dependent plasticity and train the read-out delay lines of a complex network [38].

In this paper we present circuits of neurons which function as pattern detectors and reverberators. They can be used as building blocks for networks of spiking neurons which operate on multivariate temporal patterns. The reverberating behavior is obtained by tuning the delays of synaptic connections of a circular PG to a specific pattern in a way that it responds positively only if this particular pattern arrives at its inputs, see fig. 1. Here a positive response consists of a sustained repetition of the recognized pattern. Such a circuitry of neurons fulfills short and long term mnemonic functions. Indeed, as long as the delays remain unchanged, they store the corresponding pattern as a long term memory. Furthermore, if a pattern is recognized, it reverberates through the circuit and reproduces itself over and over again until some external input switches it off or some internal saturation comes to a threshold. Thus, the stable repetition of the presented pattern may serve as a short term or working memory since the activity of the reverberator indicates that its associated pattern occurred within the immediate past.

Reverberating activity in recurrent structures is seen as one possible mechanism underlying the occurrence of repeating patterns in the brain [31, 33, 39–41]. However, it is not proven that structures as the proposed pattern reverberator occur in the brain. In section 3 we show that in principle it can be build from Hodgkin-Huxley neuron models, which suggests that it may have developed naturally as well. The chance to find the proposed conectivity is probably not very low if one considers a randomly connected network of the scale of the brain, i.e., $10^{11}$ neurons with $10^{14}$ connections [42, 43].

To illustrate our idea, we will first explain the mechanism of pattern reverberation with a description by minimalistic coincidence detector networks [see Sec. 2]. Here, analytical reasoning is possible to some extend. A numerical illustration that the main ideas can be transferred to a network of more realistic neuron models is shown in section 3. We discuss the results in Section 4 and provide an Appendix containing theoretical results on sustained activity in homogeneous delay networks.
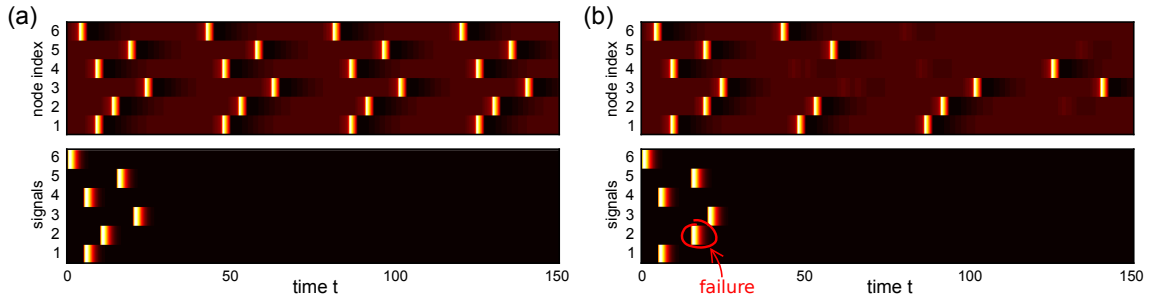
Figure 1: Activity in a single pattern reverberator consisting of six Hodgkin-Huxley neurons. The upper panel of part (a) shows a sustained activity indicated by repeated spiking (the neurons voltage traces are shown color-coded). The activation was successfully triggered by an appropriate stimulation shown in the lower panel of part (a). Part (b) shows an untimely stimulation (the pulse-signal of the second input channel is delayed) which only leads to a transient activity.

## 2 Design of a pattern reverberator

In the following we describe a pattern detector which is built as a network of spiking neurons. It is designed to determine the correct timing of spikes in a multivariate signal. This signal is a sequence of spikes arriving via different channels, i.e., at different neurons. In the following, we consider signals which are composed of exactly one spike per channel. If the correct sequence of input signals arrives at the detector it reacts with sustained activity. More specifically, it repeats the recognized sequence for a certain time.

This behavior is achieved by two essential ingredients. One is the appropriate tuning of the connection delays within the system, which are responsible for the reaction of the system to the right pattern. The second ingredient is the principle that a single pre-synaptic action potential (AP) cannot force a neuron to fire but several coincident inputs are required. This enables excluding sustained responses to wrongly timed or incomplete input sequences. We first define a simplified neuron model, which captures a neuron's capability to act as a spike coincidence detector. Similar models were introduced before, e.g., in Refs. [34, 44, 45]. Then we give some results on the possible modes of activity in networks of such neurons, which have homogeneous connection delays. This leads us to a simple design of a network, which is able to react with synchronous activity in response to a synchronous input on all channels, exclusively. For all other inputs no sustained activity can occur. Afterwards we show how the results for homogeneous delay models can be transferred to a class of models with inhomogeneous delays allowing for the detection of a large variety of multivariate inputs. Finally, we show that the detector is still functional in the case of small deviations of delay- and stimulation times from the prescribed values, which are inevitable in practical implementations.

### 2.1 A minimalistic neuron model

Whether a neuron generates an actionpotential in response to incoming stimuli depends on a number of factors as the amount and timing of stimuli, their amplitude, and the current state of the neuron, which depends on its history. Since our focus lies on a particular kind of collective

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behavior it is adequate to focus on the modeling of the essential properties responsible for this phenomenon. Many neurons have the ability to detect the coincidence of inputs [7, 12, 46, 47]. Given a set of incoming excitatory stimuli it is more likely that a neuron produces an actionpotential if the stimuli arrive within a small timeframe than if they arrive well separated. This is due to the neurons tendency to restore its resting potential after an input that did not excite the neuron above threshold. Therefore subsequent inputs cannot accumulate to a super-threshold excitation if the neuron is given enough time between them. See Fig. 2(a),(b) for an illustration in case of a Hodgkin-Huxley (HH) neuron model.

In the following, we model a single neuron as a coincidence detector, which can only assume a finite set of states. This modeling is partly motivated by an electronic implementation using FP-GAs and partly by the intention to obtain rigorous theoretical results about the dynamic behavior of the model.

We define a coincidence detector of $\nu$-th order as a finite state system in continuous time $x(t) \in \{0, ..., \nu\}$ which is able to receive quantized inputs at arbitrary points in time. An input at time $t$ leads to a reset of $x$ as:

$$x(t^+) = \begin{cases} x(t^-) + 1, & \text{if } 0 < x(t^-) < \nu, \\ 0, & \text{if } x(t^-) \in \{0, \nu\}, \end{cases} \tag{1}$$

where $x(t^\pm) = \lim_{\varepsilon \downarrow 0} x(t \pm \varepsilon)$. This means, if the neuron is not in the refractory state $x = 0$, its state is either increased by $1$ or it is immediately reset to the refractory state. Such a reset is interpreted as a spike event taking place after the state has exceeded the threshold $x = \nu$. Additionally, the relaxation of the neuron to its resting potential $x = 1$ is modeled as follows: if $x$ does not exceed the threshold after a time $\tau_e$ has passed since the input, $x$ is decreased by one. This is the basis for its functionality as a coincidence detector. Indeed, a neuron which is not in its refractory period emits a spike if and only if it has received at least $\nu$ inputs within a temporal window of width $\tau_e$. Therefore, we call $\tau_e$ the *tolerance* or *excitation time*. The *refractory period*, $\tau_r$, is the time interval where $x$ is not susceptible to inputs after it has emitted a spike. This means that if $x$ emits a spike at time $t$, it will switch from the state $x(t + \tau_r^-) = 0$ to $x(t + \tau_r^+) = 1$ at time $t + \tau_r$. During the interval $(t, t + \tau_r)$ the neuron remains at $x = 0$ unresponsive to the external inputs.

In the case $\tau_e < \tau_r$ the described model can be formalized as follows:

$$\dot{x}(t) = \sum_{t_j} \left[ \left( \chi_{[1,\nu-1]} - \nu\chi_{\{\nu\}} \right) \delta(t - t_j) - \chi_{[2,\nu]}\delta(t - t_j - \tau_e) + \delta(t - t_j - \tau_r) \right], \tag{2}$$

where $t_j$ are the times of external pulses arriving and $\chi_I$ is the indicator function such that $\chi_I = 1$ for $x(t^-) \in I$ and $\chi_I = 0$ otherwise. The delta-function $a\delta(t - t_*)$ denotes the jump of the solution $x(t_*^+) = x(t_*^-) + a$. From Eq. (2) it is evident that this model possesses time-delays $\tau_e$ and $\tau_r$, and its evolution is determined by the history interval of the length $\max\{\tau_e, \tau_r\}$. In the case $\tau_e > \tau_r$, an additional component of the dynamics must be taken into account, which is not covered by Eq. (2), i.e., when the excitation decay at time $t_j + \tau_e$ appears to follow some refractory interval caused by a later spike, that is $t_j + \tau_e > t_{j+k} + \tau_r$. In such a case, the decay term $\chi_{[2,\nu]}\delta(t - t_j - \tau_e)$ has to be disregarded.
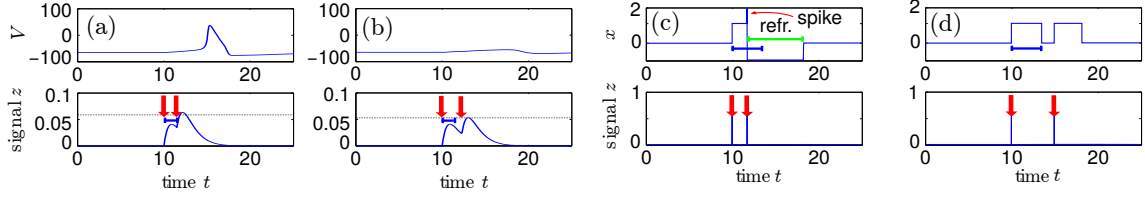
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Figure 2: Comparison of a Hodgkin-Huxley neuron [(a) and (b)] and the minimal model (2) for a coincidence detector of second order [(c) and (d)]. Both models exhibit a tolerance time $\tau_e$ (indicated by a blue bar) which represents an upper bound of the interspike interval of two arriving stimuli which trigger a postsynaptic spike.

Figure 2 compares the responses of the coincidence detector and a more realistic HH neuron model on two subsequent pulse inputs. If the time interval between the inputs is smaller than $\tau_e$ [Figs. 2(a) and (c)] then a spike is emitted. Otherwise, the system is not responding with a spike [Figs. 2(b) and (d)]. Details of the chosen parameters for the HH model are given in Appendix E.

## 2.2   Sequence detection by networks of coupled coincidence detectors

To construct a detector for a multivariate spike sequence with $N$ channels we consider a network of coincidence detectors with delayed interactions between its units $x_j$, $j = 1, ..., N$. If $x_j$ is coupled into $x_i$, a spike emitted by $x_j$ at time $t$ arrives as an input at the postsynaptic element $x_i$ at time $t + \tau_{i,j}$, where $\tau_{i,j} \geq 0$ is the propagation delay from $x_j$ to $x_i$. At the moment of the input arrival the state of the postsynaptic element $x_i$ is reset according to Eqn. (1).

The generation of a spike by $x_i$ requires that at least $\nu$ predecessors have spiked polysynchronously with respect to $x_i$, which means that their inputs arrive at $x_i$ simultaneously within a time interval of width $\tau_e$. We assume that each of the $N$ elements acts as a receptor for one signal channel. This means, whenever an external signal of type $j \in \{1, ..., N\}$ arrives at some time $t$, the corresponding element $x_j$ instantaneously emits a spike and is reset to $x_j(t^+) = 0$. Concerning this external signal, there is no subthreshold excitation, i.e. it acts like a bundle of at least $\nu$ simultaneous presynaptic inputs.

We assume that a successful recognition corresponds to an increased activity of the network and take this increased activity to correspond to indefinitely sustained activity in the simplified model. Hence, we say that a sequence of external inputs is accepted if the system's response is a sustained activity. Otherwise, i.e. if the response activity is only transient and dies out after finite time, the system is said to have rejected the input sequence. Our aim is to design a coupling structure which accepts exactly one desired sequence, where perturbations of the input sequence should be accepted within some tolerance bound. Other inputs should be rejected. We assume that the sequence which is to be recognized has the form $\boldsymbol{s} = (s_1, ..., s_N)$, where each entry $s_j \geq 0$ corresponds to an input time moment from the channel $j$.

## 2.3 Sustained activity in a regular network with homogeneous delays

Let us now consider how to achieve the desired behavior of the network, i.e. that it responds to a specific pattern with a sustained activity. For the beginning we assume that all delays $\tau_{i,j} \equiv \tau_0$ are the same and that the pattern to be recognized is the synchronous sequence $s_0 = (0, ..., 0)$. After the initial simultaneous external stimulation of all elements at time $t_0$, all elements emit spikes, which arrive at their successors at time $t_0 + \tau_0$. Since we wish that the system reacts by sustained activity, it is obviously necessary that $\tau_0 > \tau_r$. Otherwise the elements are in refractory state at time $t_0 + \tau_0$, no new spikes are emitted and the network remains silent afterward. Furthermore, it is clear that sustained *synchronous* spiking of all neurons is possible if and only if each neuron has an in-degree $d_{\mathrm{in}}$ equal to or larger than the coincidence order $\nu$. This synchronous spiking mode is then triggered by a stimulation with the sequence $s_0$. A more general result about the possibility of sustained activity is proven in Appendix A, where we explore conditions under which the existence of an *activity core* is a sufficient [Proposition A.1] or even necessary and sufficient condition [Proposition A.2] for the existence of sustained activity. The activity core is defined as the maximal subset $\mathcal{A} \subset \{1, ..., N\}$ of nodes which fulfills

$$\mathcal{A} = \left\{ j \mid d_{\mathrm{in}}(j)_{|\mathcal{A}} \geq \nu \right\}, \tag{3}$$

where $d_{\mathrm{in}}(j)_{|\mathcal{A}}$ is the restricted in-degree of the unit $x_j$ with respect to connections from other units in $\mathcal{A}$ only.

To preclude the synchronous mode to be activated by a stimulation different from $s_0$ (up to a certain error tolerance of order $\tau_e$), we stipulate that all in-degrees equal to the coincidence order

$$d_{in}(j) = \nu. \tag{4}$$

For networks fulfilling (4), we show that for sufficiently small tolerance time $\tau_e$ the synchronous mode is the only possible mode of sustained activity for the network if the sequence

$$\{j\} \to \mathrm{Pre}(\{j\}) \to \mathrm{Pre}(\mathrm{Pre}(\{j\})) \to ... \tag{5}$$

becomes stationary at $\{1, ..., N\}$ for all $j$. Here $\mathrm{Pre}(A)$ denotes the predecessors of a subset $A$

$$\mathrm{Pre}(A) := \{x_k \mid \exists x_j \in A : x_k \to x_j\}.$$

The proof is given in the Appendix C, Proposition C.3. Perhaps more intuitively, the stationarity of (5) for all $j$ means that for large enough $m$ there must exist paths of length $m$ between each pair of nodes. This means, the network is strongly connected and the greatest common divisor (GCD) of all cycle lengths is one. It has been studied in [48] how the GCD is related to synchronized clusters and global synchronization in the case $\nu = 1$.

Note that if $\tau_0$ is large enough ($\tau_0 > 2\tau_r$) there may formally exist distinct sustained synchronous solutions which consist of a periodically repeated series of synchronous spikes where the interspike intervals are larger than the refractory period $\tau_r$ and the period is at most $\tau_0$. The fact, that multiple coexisting solutions appear with increasing $\tau_0$, is a general property of systems with time delays [49]. However, only one of these distinct solutions (the one with uniform interspike interval $\tau_0$) can be triggered by a single stimulation sequence.
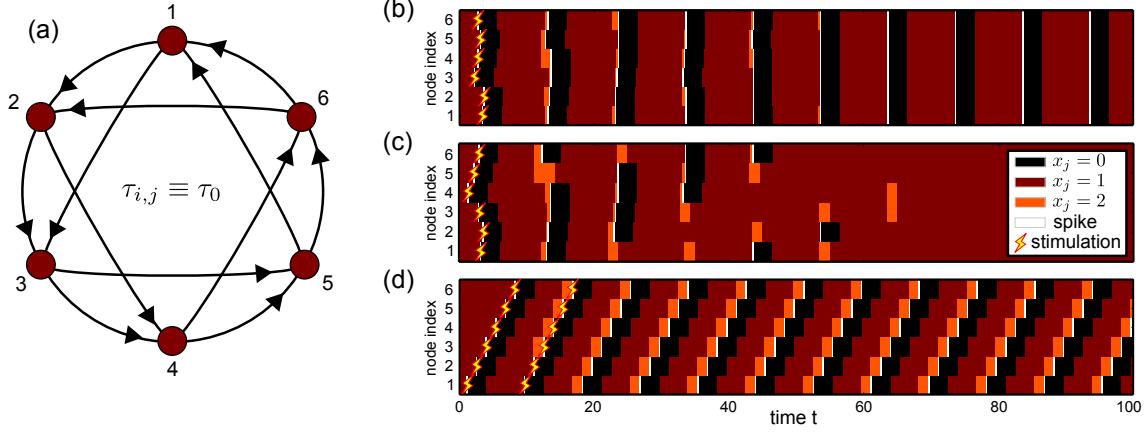
Figure 3: A single network of $N = 6$ coincidence detectors with order $\nu = 2$, refractory time $\tau_r = 3$, tolerance time $\tau_e = 1.5$, and homogeneous delays $\tau_0 = 10$. (a) Connection scheme; (b)–(d) Possible stimulation induced responses of the network. (b) Stimulation at nearly synchronous times (first excitations) leading to convergence to synchronous firing in finite time; (c) A too large perturbation leads only to transient activity. (d) Applying a wave-like stimulation pattern twice induces a sustained rotating wave.

## 2.4  Detection of the synchronous sequence by a unidirectional ring

Motivated by the previous observations we now give a concrete example for a circuit of units with coincidence order $\nu = 2$, see Fig. 3. To achieve a homogeneous in-degree $d_{in}(j) = 2$ for each node $j$ we select as predecessors the nodes $j - 1$ and $j - 2$ (modulo $N$). As a result we obtain a unidirectional ring where each unit connects to its nearest and next-nearest neighbors in one direction, see Fig. 3(a). In this network, a sustained synchronous spiking of all nodes can be excited by a synchronous stimulation of all nodes, see Fig. 3(b). There, the time-dependent evolution of each node is color-coded as indicated in the legend, where the spikes are marked by white lines followed by the refractory period $x_j = 0$ of the length $\tau_r$ shown in black. The resting state, $x_j = 1$, is indicated by red and the excited state, $x_j = 2$, by orange color.

Since $\mathcal{A} = \{1, ..., N\}$ and all delays are identical, the network recognizes the input sequence $s_0$. Moreover, if a non-synchronous sequence $s = s_0 + \eta$ is applied, the network will still react with a sustained activity as long as the initial activation times of neighboring nodes do not deviate more than

$$|s_j - s_{j-1}| = |\eta_j - \eta_{j-1}| < \tau_e, \ j = 1, ..., N. \tag{6}$$

In Figure 3(b)–(d) we show some possible responses of the network to different stimulations. As long as $\tau_e > \tau_r/N$, and $\tau_e > \tau_0/(N + 1)$, a wave-like, non-synchronous sustained activity is possible [see Fig. 3(d)]. However, this mode can not be induced by a sequence with one pulse per channel. It seems that for such sequences, either synchronous activity is induced, or, if (6) is violated, the activity dies out after a transient.

The dynamics in the unidirectional ring with delayed connections resembles the one reported in [50–55], where also the coexistence of stable synchronous and rotating waves are reported. This is due to the symmetry properties of the considered scheme and the time delays. However,
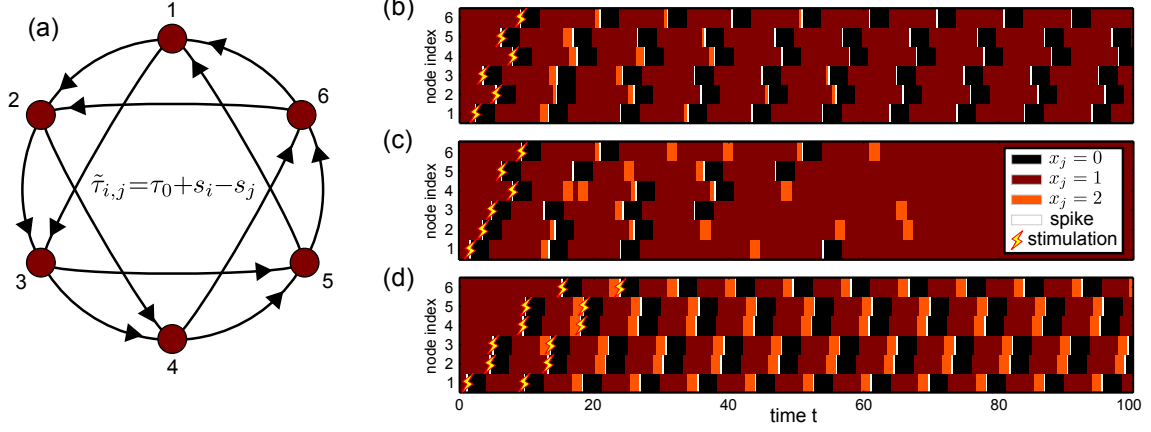
Figure 4: A network of $N = 6$ coincidence detectors with parameters as in Fig. 3. The delays $\tilde{\tau}_{i,j}$ are tuned according to (7) with the sequence $s = (0, 2, 1, 4, 3, 7)$ and a base delay $\tau_{i,j} \equiv \tau_0 = 10$. (a) Connection scheme; (b)–(d) Possible stimulation induced responses of the network. (b) Stimulation at times close to the pattern $s$ leads to convergence to an exact reverberation of the pattern; (c) A larger perturbation leads only to transient activity. (d) The rotating wave solution of the system with homogeneous delays [cf. Fig. 3(d)] exists in a transformed form in the system with heterogeneous delays $\tilde{\tau}_{i,j}$ as well.

in contrast to these results, which were obtained for oscillating units, our setup employs excitable systems with a coincidence order $\nu$ and leads to the coexistence of a sustained spiking state and a stable quiescence state.

## 2.5 Recognition of asynchronous patterns

We have shown how a pattern reverberator for a synchronous pattern $s_0 = (0, ..., 0)$ can be constructed. In fact, this provides us with all necessary information about the construction of a reverberator for an arbitrary sequence $s = (s_1, ..., s_N)$. Indeed, if we already possess a system which can recognize the synchronous sequence, then a system, which can recognize the sequence $s$ can be constructed by a modification of the connection delays. To be more precise, defining new delays

$$\tilde{\tau}_{i,j} = \tau_{i,j} + s_i - s_j \tag{7}$$

leads to a system which reacts with sustained activity for sequences sufficiently close to $s$ [see Fig. 4].

Both systems, the one with delays $\tau_{i,j}$ and the one with delays $\tilde{\tau}_{i,j}$ are dynamically equivalent. A solution $x(t)$ of the original system is transformed into a solution $y(t)$ of the one tuned to $s$ by the componentwise timeshift $y_j(t) = x_j(t - s_j)$. For instance, a sustained activity corresponding to the rotating wave shown in Fig. 3(d) is present in the system with delays (7) as shown in Fig. 4(d). For details and other examples for the application of this *componentwise timeshift tranformation* see [56–59]. In particular, if the global synchronous spiking is the only possible mode of sustained activity in the detector for $s_0$, the sustained reverberation of the pattern $s$ is the only possible sustained mode in the system with inhomogeneous delays $\tilde{\tau}_{i,j}$.
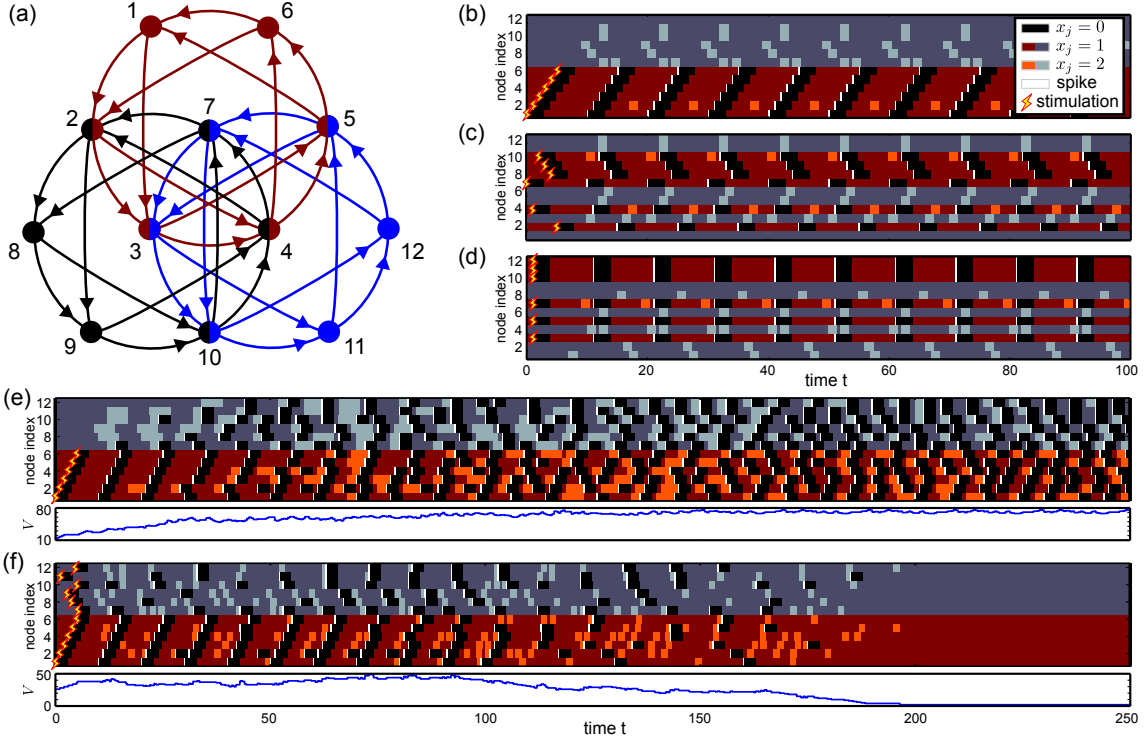
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Figure 5: A network of $N = 12$ coincidence detectors with parameters as in Figs. 3. (a) The connection scheme is a combination of three single pattern reverberators as in Fig. 4, consisting of the nodes $\boldsymbol{g}_1$ (red), $\boldsymbol{g}_2$ (black), and $\boldsymbol{g}_3$ (blue). Each group is tuned to a different pattern: $\boldsymbol{s}_1$, $\boldsymbol{s}_2$, and $\boldsymbol{s}_3$ [see main text for details]. (b)–(f) Stimulation induced responses of the network. (b) Stimulation of $\boldsymbol{g}_1$ with $\boldsymbol{s}_1$; (c) Stimulation of $\boldsymbol{g}_2$ with $\boldsymbol{s}_2$; (d) Stimulation of the $\boldsymbol{g}_3$ with $\boldsymbol{s}_3$. (e) For increased tolerance time $\tau_e = 5$ an initial activation of $\boldsymbol{g}_1$ with $\boldsymbol{s}_1$ leads to a sustained mode of activation involving all nodes. Below the color-plot, the time trace of the activity measure $V(t)$ is shown, see Appendix D; (f) Transient response after stimulation of $\boldsymbol{g}_1$ with $\boldsymbol{s}_1$ and randomly chosen stimulations at all other nodes.

## 2.6    Encoding multiple patterns in coupled coincidence reverberators

It is possible to couple several single interleaving pattern reverberators of the type shown in Fig. 3 into one larger network where each reverberator shares some of its nodes with others, see Fig. 5(a). The connection delays within each of the three groups, consisting of the nodes $\boldsymbol{g}_1 = (1, 2, 3, 4, 5, 6)$, $\boldsymbol{g}_2 = (2, 8, 9, 10, 4, 7)$, and $\boldsymbol{g}_3 = (7, 3, 10, 11, 12, 5)$, have been adjusted according to (7) to tune each group to a different pattern. The patterns were chosen as $\boldsymbol{s}_1 = (0, 1, 2, 3, 4, 5)$, $\boldsymbol{s}_2 = (5, 4, 3, 2, 1, 0)$, and $\boldsymbol{s}_3 = (0, ..., 0)$. For appropriate choices of $\tau_e$, $\tau_r$, and $\tau_0$, the resulting network is able to recognize the different patterns as shown in Fig. 5(b)–(d). Each of these panels shows the networks response to an initial stimulation of a different group. To distinguish nodes which are not members of the stimulated group we selected a dimmed colormap.

However, the additional connections may allow for additional sustained activity involving nodes from different pattern reverberators. This is illustrated in Fig. 5(e), where the pattern of the first group (red color in 5(a)) is initially applied. For that example, the tolerance $\tau_e$ was increased to $\tau_e = 5$ to induce the effect of so-called "crosstalk" between the patterns. Such crosstalk can

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prevent successful activation or discrimination of sequences. It may arise either directly due to the additional connections within each group or indirectly due to the rebounding influence from collateral activation of nodes which are not part of the initially activated group (as in Fig. 5(e)). In both cases the usual activation sequence may be disrupted by a too early invocation of a spike due to the increased amount of input. This can either cause the excitation to die out completely or to cause an activation of larger parts of the network and possibly impeding discrimination of different stimulation patterns by the lack of corresponding attractors.

The phenomenon of disrupting crosstalk can almost always be overcome if the sensitivity of the coincidence detectors is increased, i.e., $\tau_e$ is decreased. However, this is not possible to an arbitrary amount for real neurons and requires a trade-off with the robustness of the device since a decreased $\tau_e$ directly decreases the tolerance of the detector for perturbations of the pattern. An example, where an additional initial activation disrupts a pattern and eventually leads to a total decay of activity is illustrated in Fig. 5(f), where the pattern of the first group is applied as a subsequence of the stimulation but does not induce a sustained response. Note that the transient time is much longer in this situation than for single reverberator, cf. Fig. 4(b). It is also worth mentioning that, if an initial stimulation is applied to all nodes, sustained activity different from the responses shown in Fig. 5(b)–(d) is possible already for the tolerance time $\tau_e = 1.5$. However, if $\tau_e$ is decreased further, such an activity could not be observed in simulations, while the positive responses to the different pattern persist.

To conclude, in a network of interleaving pattern reverberators, the relation between stimulus and positive response is altered in several important ways with respect to a single reverberator as constructed in Secs. 2.4 and 2.5. Firstly, an input may lead to a sustained response which doesn't repeat the same sequence of pulses. Indeed, if a stimulus triggers sustained activity in one pattern reverberator, other neurons not belonging to that reverberator may be activated spuriously as a side effect of the activity of the activated pattern or a completely different pattern may evolve as in Fig. 5(e). Secondly, there may exist several different stimuli which lead to one and the same sustained activity. Even an incomplete delivery of one of the encoded patterns can trigger reverberating activity if the missing external stimuli are compensated by the timely stimulation of some neurons from a different pattern which are predecessors to the neuron at the site of missing direct stimulation. Thus, the one-to-one correspondence between input patterns and sustained responses is lost.

## Perturbed delays

One last theoretical consideration has to be taken in view of physical implementations of the proposed system. In real systems one cannot expect delay times to be reliable in taking exact values. Therefore, to justify the model and to obtain a stably working electronic device, it is important to take into account imperfections of the implementation with respect to the delay values.

In the Appendix B, we prove that if $d_{\mathrm{in}} \equiv \nu$, the synchronous solution is super-stable in the case of homogeneous delays and that a nearly synchronous sustained activity persists if the delay times are weakly perturbed. These results transfer to a system with non-homogeneous delays (7) obtained from one with weakly perturbed, nearly identical delays.
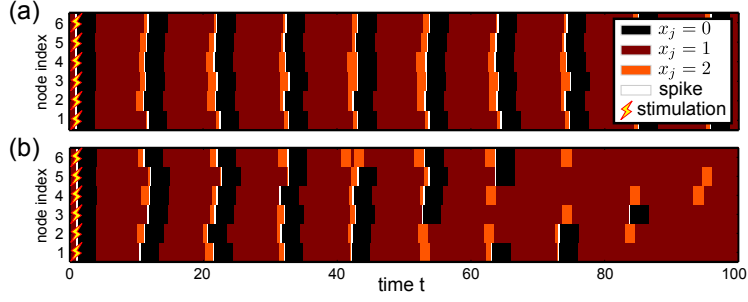
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Figure 6: Response dynamics of a single pattern reverberator for the synchronous sequence $s_0$ with slightly perturbed delay times $\tau_{i,j} = \tau_0 + \eta_{i,j}$, $\eta_{i,j} \in [-1, 1]$; parameters are as in Fig. 3. (a) and (b) show the response for two different samples of the delays, where the sample in (a) allows for sustained activity, but in (b) the pattern recognition fails.

In Fig. 6, for two realizations of perturbed delays, we show the response of a single reverberator, as in Fig. 3 with $\tau_{i,j} = \tau_0 + \eta_{i,j}$, in response to the synchronous stimulation. Here, the perturbations $\eta_{i,j}$ are uniformly distributed within $[-1, 1]$, which can also lead to failure as shown in panel (b). Similar as for perturbed initial stimulation times, the system becomes more robust with respect to perturbations of the delays if the tolerance time $\tau_e$ is increased.

## 3  Simulation with Hodgkin-Huxley Neurons

In this section we will adopt the networks, which were developed in the previous section, to design pattern reverberators based on Hodgkin-Huxley neurons[60]. Each neuron is described by the equations given in Appendix E. The dynamic equation for the membrane potential has the form

$$\dot{V}(t) = -g_{Na}m(t)^3h(t)(V(t)-V_{Na})-g_Kn(t)^4(V(t)-V_K)-g_l(V(t)-V_l)-z(t)(V(t)-V_r)$$

where $z(t)$ is the synaptic input. In absence of input ($z(t) = 0$) the system has a globally stable fixed point with at the resting potential $V_0 \approx -65$mV. For the simulations, we initialize a HH neuron in this resting state and apply an input signal $z(t) = \gamma p(t - t_0)$ at time $t = t_0$. Here, we emulate the excitatory postsynaptic potential (EPSP) as the $\alpha$-function

$$p(t) = t \exp(-t/\alpha) \tag{8}$$

with $\alpha = 0.9$ [see Fig. 7]. Numerically we determine the critical value $\gamma_c$ of the pulse intensity which causes a spike in a resting neuron as $\gamma_c \approx 0.077$. Operating with an intensity of $\gamma = 0.05$, we find that the corresponding tolerance time is given as $\tau_e \approx 2.27$ms, i.e., if two pulses of intensity $\gamma$ arrive at a time difference smaller than $\tau_e$, the neuron will emit a spike in response, otherwise it remains silent [see Fig. 2 (a)].

We have constructed a single pattern reverberator of $N = 6$ HH-neurons coupled as depicted in Fig. 4(a) with base delay $\tau_0 = 35$ms and tuned to the pattern $s = (5, 10, 20, 5, 15, 0)$. Figure 1 shows the responses of such a detector to stimuli. Further, we have conducted numerical
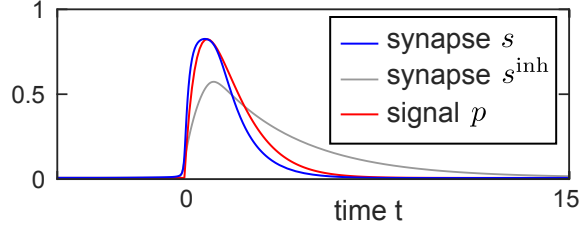
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Figure 7: Comparison of the pulsatile signal $p(t)$ [see Eq. (8)], and PSPs of the excitatory synapse $s(t)$ and the inhibitory synapse $s^{\mathrm{inh}}(t)$ generated by the HH model, see App. E, Eqs. (18).

experiments for three coupled single detectors as shown in Fig. 5. The delays on the connections were chosen according to (7) for three different patterns and base delay $\tau_0 = 35$ms. In Fig. 8 we show that this network consisting of twelve HH neurons reacts with sustained activity to each of the patterns. For two of the patterns [(a) and (c)] the response is a periodic reproduction of the applied pattern. In Plot (b) the applied pattern is repeated but the network also exhibits spurious activations of nodes [$1, 3, 5,$ and $6$, indicated by red pencil marks], which are not part of the stimulated group.

To some extend, these spurious activations can be overcome by adding an inhibitory aftershot following each EPSP. This may be done by including an inhibitory connection with a slightly larger delay $\tau_{i,j}^{\mathrm{inh}} = \tau_{i,j} + \tau_{\mathrm{inh}}$ [variable $s^{\mathrm{inh}}(t)$ in the HH equations (18)]. We illustrate this in Fig. 8(d), where we included inhibitory synapses [see Fig. 7(d)] with an additional lag $\tau_{\mathrm{inh}} = 1$ms to stabilize the pattern $s_2$. Some primary spurious activations are still present but they are surpressed in the following reverberations of the applied pattern due to the additional inhibitory connections. The inhibitory aftershot effectively decreases the tolerance time $\tau_e$ of the connection, leading to a higher precision of the coincidence detection.

# 4   Discussion

In the present paper we have shown how ensembles of coupled spiking elements can detect and reverberate activation patterns. We have focused on a special coupling structure which serves this purpose. This was illustrated for networks composed of simple, idealized coincidence detectors as well as for networks of HH neuron models. The proposed systems may serve as elements of neural computation in biological and engineered setups by providing an implementation of working memory or building blocks of larger processing devices.

Due to the potential complexity of coincidence detector networks in general, many questions arise when the assumptions made in this work are relaxed.

Let us first turn to a question, which has a well-known answer: How can the setup be adapted to recognize stimulation sequences, which do not necessarily deliver maximally one input pulse per channel? In fact, the proposed detectors can be equipped with a "preprocessor", which transforms a given temporal sequence of pulses on one channel into a single spike. This is accomplished by projecting the preprocessor neuron via an array of delay lines to a detector
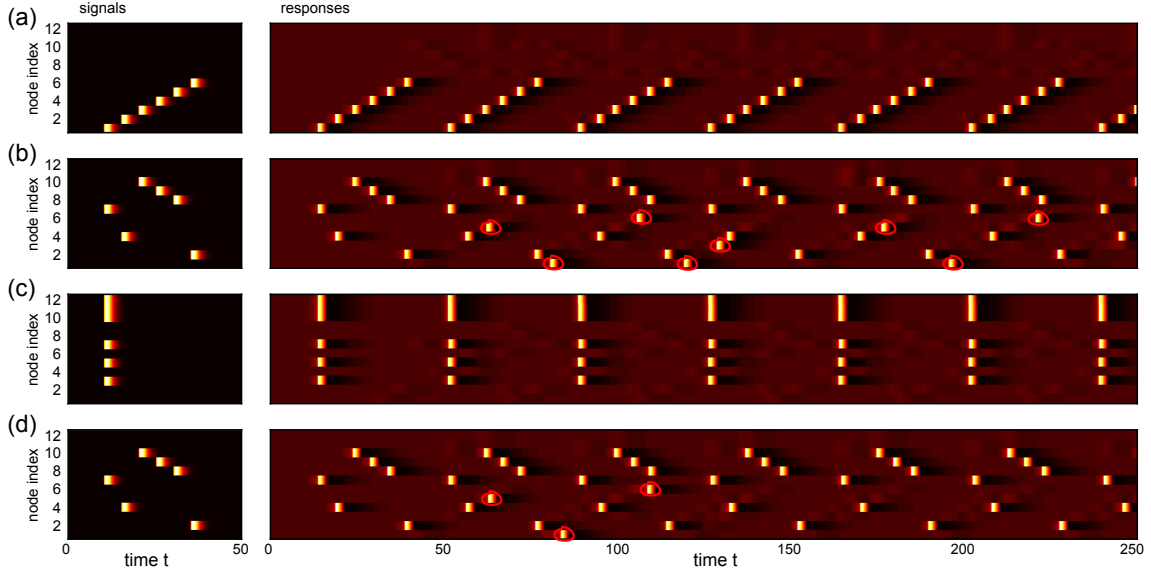
Figure 8: (a)–(c) Activity of three overlapping cyclic pattern reverberators consisting of twelve Hodgkin-Huxley neurons with delayed connections tuned to the patterns $\boldsymbol{s}_1 = (0, 5, 10, 15, 20, 25)$, $\boldsymbol{s}_2 = (25, 20, 15, 10, 5, 0)$, and $\boldsymbol{s}_3 = (0, ..., 0)$ with base delay $\tau_0 = 35$ms [see Fig. 5 for the connection scheme and Eq. (7) for the choice of the delays $\tau_{i,j}$]. The right panels show the reverberating responses following an initial stimulation with sequences (a) $\boldsymbol{s}_1$; (b) $\boldsymbol{s}_2$; (c) $\boldsymbol{s}_3$. The applied signals are shown in the left panels. Plot (d) shows the response to $\boldsymbol{s}_2$ in the presence of additional inhibitory connections with delays $\tau_{i,j}^{\mathrm{inh}} = \tau_{i,j} + 1$ms. Failures in the reproduction of the pattern are indicated by red pencil marks.

whose order equals the number of pulses in the corresponding channel. The delays are chosen such that the relayed signals arrive synchronously at the detector if they were delivered with the correct timing. Such setups were considered in Refs. [15, 38, 61].

In the examples shown in the present work we have always considered an identical order $\nu = 2$ for all coincidence detectors of the network. However, the effects of a higher order $\nu > 2$ and also of variability of the order within the network are interesting subjects to further studies. The theoretical results, which were proven in the appendix, are already obtained for networks of arbitrary order $\nu$, and they appear to be generalizable to variable orders $\nu = \nu_j$. From an increased coincidence order $\nu > 2$ one might expect that for a network the effect of crosstalk is less pronounced, since a larger number of interfering inputs is needed to evoke a mistimed response. This may result in an increased storage capacity, measured as the number of stored patterns divided by the number of nodes. This is because an increased value of $\nu$ requires a more precise polysynchrony of the whole network. To induce a spike in a neuron, $\nu$ of its predecessors must have emitted spikes that arrive within a time window of size $\tau_e$, which imposes a stronger constraint on the networks polysynchrony for larger $\nu$. For instance, the tolerance condition (6) for a ring shaped detector would tighten to

$$\max_{i \in \{j-1, j-2\}} \left| s_i - s_j \right| < \tau_e,$$

if the coincidence order of the nodes would be increased to $\nu = 3$ and $x_{j-3}$ would be added

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to the predecessors of $x_j$. If two nodes have no common successor, their initial activations may deviate further than $\tau_e$ while the network still responds with sustained synchrony. Here, the maximal allowed deviation $\max_{1 \leq j,k \leq N} |s_j - s_k|$ seems to be connected to the number $m_0 \in \mathbb{N}$, where the sequence (5) becomes stationary at $\{1, ..., N\}$ [cf. proof of Prop. C.3]. For larger $\nu$, one usually obtains a lower $m_0$.

Another potential generalization of the coupling structure„ is to choose $d_{in} > \nu$ for each single detector to increase its robustness. In this case again the general principle applies that an increased robustness comes with a loss of precision, since a larger in-degree allows for an activation of a pattern by an incomplete stimulus. From another point of view this could also been rated beneficial since it allows for pattern completion.

It is evident that at least for the case that $\nu > 2$ coincidence detectors of the form (1) do not completely describe the corresponding response dynamics of a neuron. This is because a coincidence detector emits a spike if and only if within a tolerance frame of length $\tau_e$ it has received $\nu$ inputs. In case of a neuron, the internal timing of the arriving APs may also play a role in determining whether the neuron will generate an AP in response. Even for the case $\nu = 2$ the idealized model may disregard some resonance effects of the inputs.

Further, the role of inhibitory connections, which we mentioned only shortly, should be studied to more detail in the future. Additionally to their stabilizing effects for single patterns they might play a role in preventing runaway excitation in larger networks. Another possible function of inhibitory connections could be a specific inhibition of concurring patterns during the activation of another pattern.
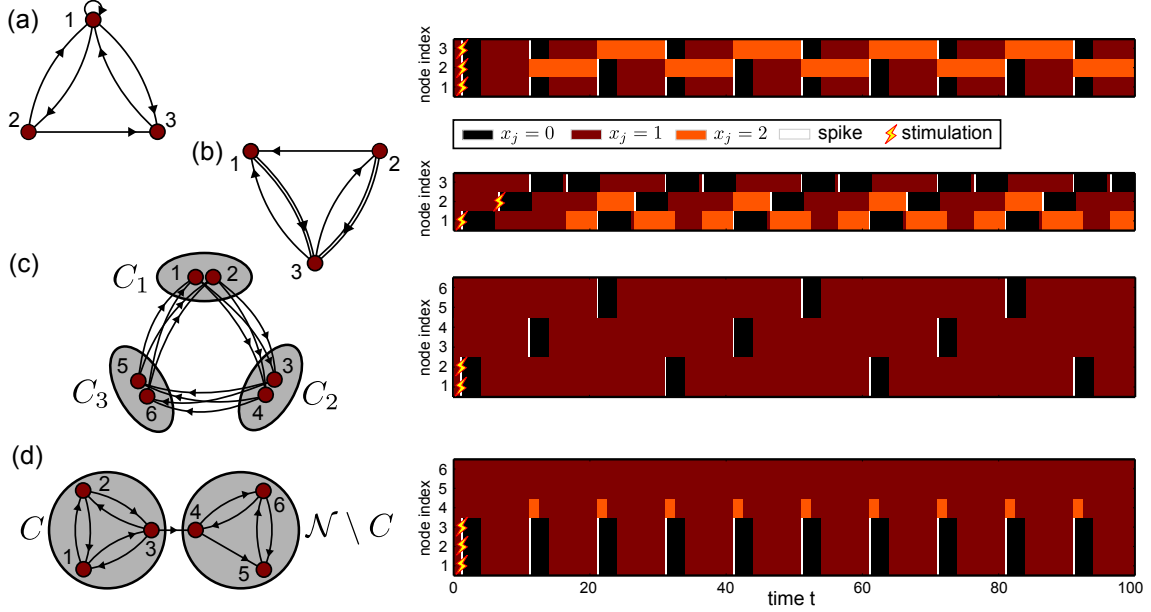
Figure 9: Contrasting examples for Prop. A.2 [(a), (b)] and Prop. C.3 [(c), (d)]. On the left hand the coupling schemes are depicted; on the right, sustained activity different from complete synchronization is shown. The initial excitation is induced external signal to the nodes: (a), (d) $\{1, 2, 3\}$; (b), (c) $\{1, 2\}$. For all cases, we have $\nu = 2$ and $\tau_0 = 10$. In (a) $\tau_e = 11$, $\tau_r = 3$; (b) $\tau_e = 6$, $\tau_r = 5$, and $s = 5.5$ [see text] (c), (d) $\tau_e = 1.5$, $\tau_r = 3$.

# Appendix

## A    The activity core in a network with homogeneous delays

In the following, we consider a network of coincidence detectors as introduced in Sec. 2 with homogeneous delays $\tau_{j,i} \equiv \tau_0$. Its activity core $\mathcal{A}$, as defined in Eq. (3), can be constructed iteratively as the stationary point of the sequence

$$\mathcal{N}_1 = \mathcal{N} := \{1, ..., N\} \text{ and } \mathcal{N}_{k+1} := \left\{ x_j \mid d_{\text{in}}(x_j)_{|\mathcal{N}_k} \geq \nu \right\}. \tag{9}$$

For $\mathcal{A} \neq \emptyset$, synchronous activity obviously persists on this set. Thus, $\mathcal{A} = \emptyset$ is a necessary condition for all activity to die out after a stimulation with the synchronous sequence $s_0$. However, if $\tau_e > \tau_0$, it is not sufficient. To see that, consider for the case $\nu = 2$ the simple 3-node network depicted in Fig. 9(a) with links

$$x_1 \to \{x_1, x_2, x_3\}, \ x_2 \to \{x_1, x_3\}, \ x_3 \to x_1.$$

It has $\mathcal{A} = \emptyset$, but if $\tau_e > \tau_0$ there exists a sustained activity, where at each time $t = t_0 + 2k\tau_0$, $x_1$ and $x_2$ fire and $x_3(t) = 2$ is excited only at subthreshold-level, and at times $t = t_0 + (2k + 1)\tau_0$, $x_1$ and $x_3$ fire and $x_2(t) = 2$. The following statement holds for the case $\tau_e < \tau_0$:

**Proposition A.1.** *If $\tau_e < \tau_0$ and $\tau_r < \tau_0$, a sustained activity as a response to the synchronous input can persists indefinitely if and only if $\mathcal{A} \neq \emptyset$.*

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*Proof.* We already know that for $\mathcal{A} \neq \emptyset$ sustained activity exists. Thus we only need to show that no sustained activity is possible if $\mathcal{A} = \emptyset$ and $\tau_e < \tau_0$.

Let us first assume that the activity is initiated by a synchronous stimulation at $t = t_0$. If $\mathcal{A} = \emptyset$ there exists at least one node $x$ with $d_{\mathrm{in}}(x) < \nu$. This node and all other nodes $x_j$ with $d_{\mathrm{in}}(x_j) < \nu$ do not emit a spike at $t = t_0 + \tau_0$ and never later, since their excitation level, which is $x_j(t) = d_{\mathrm{in}}(x_j)$ at time $t = (t_0 + \tau_0)^+$ drops back to $x_j(t) = 0$ until $t = (t_0 + 2\tau_0)^-$ due to $\tau_e < \tau_0$. Therefore, all nodes $x_j$ with $d_{\mathrm{in}}(x_j) < \nu$ will never spike and we can exclude them from considerations. All nodes with $d_{\mathrm{in}}(x_j) \geq \nu$ will spike at time $t = t_0 + \tau_0$ since they receive $d_{\mathrm{in}}(x_j) \geq \nu$ inputs. The set of these latter nodes is just $\mathcal{N}_1$ from (9). At the next relevant instance at $t = t_0 + 2\tau_0$, all nodes in the set $\mathcal{N}_2 = \{x_j \mid d_{\mathrm{in}}(x_j)_{|\mathcal{N}_1} \geq \nu\}$ fire, and so on. Since $\mathcal{N}_k$ becomes stationary at $\emptyset$ at latest in the $N$-th step, all spiking activity will cease at $t = t_0 + N\tau_0$. $\qquad\square$

A natural question is whether Proposition A.1 can be generalized to arbitrary sustained activity: Is it true that no sustained activity is possible if the activity core is empty? Without further qualification, this conjecture is wrong. To see that consider $\nu = 2$ and the 3-node network [Fig. 9(b)]

$$x_1 \rightrightarrows x_3, \; x_2 \rightrightarrows x_3, \; x_2 \to x_1, \; x_3 \to \{x_1, x_2\},$$

where the double arrow denotes a connection of double impact, e.g. a solitary spike of $x_1$ at time $t$ already induces a spike of $x_3$ at $t + \tau_0$ (an equivalent network can easily be constructed by replacing each node which emits double spikes by two with the same in- and outgoing links of single strength). Clearly, the network has an empty activity core and the response to a synchronous stimulation dies out according to Prop. A.1. However, the response to a stimulation of $x_1$ at $t = t_0$ and $x_2$ at $t = t_0 + s$ may be sustained. In fact, if the duration of the refractory period $\tau_r$, and the tolerance $\tau_e$ fulfill $\tau_r < s < \tau_e$, then $x_3$ will emit two spikes at times $t_0 + \tau_0$ and $t_0 + \tau_0 + s$. Further, $x_1$ is excited to $x_1(t_0 + \tau_0 + s)^+ = 2$ via the input from $x_2$. The first spike emitted by $x_3$ arrives at $x_1$ at time $t_0 + 2\tau_0$ which causes $x_1$ to spike if it is still excited at this time, i.e. $x_1(t_0 + 2\tau_0) = 2$. This is the case if $\tau_0 - s < \tau_e$ (and because $\tau_r < \tau_0$). The spike arrives at $x_2$ at the same time but only excites $x_2$. Only the second spike, which arrives at $t = t_0 + 2\tau_0 + s$, causes $x_2$ to fire and excites $x_1$. Then the cycle starts again (the excitation of $x_1$ will be decayed until the next spike arrives at $t_0 + 3\tau_0 + s$ since $\tau_r < \tau_0$). The dynamics can be seen in Fig. 9(b), right panel.

The construction of the example relied on $\tau_r < \tau_e$. And indeed, if we assume the contrary, we obtain an assertion independent of the initial stimulation:

**Proposition A.2.** *If $\tau_e < \tau_r < \tau_0$, sustained activity can persist indefinitely if and only if $\mathcal{A} \neq \emptyset$.*

*Proof.* In general, if a node $x_j$ with $d_{\mathrm{in}}(x_j) \leq \nu$ spikes, then at least one of its direct predecessors must have spiked twice in an interval of length $\tau_e$. This is impossible if $\tau_e < \tau_r$. $\qquad\square$

# B   Stability of the synchronous firing mode and perturbed delay times

**Proposition B.1.** *Consider a network with homogeneous in-degree $d_{\mathrm{in}} \equiv \nu$. If for homogeneous delay times $\tau_{i,j} \equiv \tau_0$ for all $j \in \mathrm{Pre}(\{i\})$ a sustained synchronous firing mode exists, then a nearly synchronous, sustained mode persists for sufficiently small perturbations of the delay-times.*

*Proof.* Consider weakly perturbed delays

$$\tau_{j,i} = \tau_0 + \mathcal{O}\left(\varepsilon\right),$$

where $\varepsilon > 0$ is the perturbation size. Initially, the system is assumed to be in its resting state $x_j(t) = 0$, $j = 1, ..., N$, for $t < t_0$. Then, a stimulation is applied at times $t_0^j = t_0 + \mathcal{O}\left(\varepsilon\right)$ which are nearly synchronous. The $m$-th spike time of the $j$-th element is denoted by $t_m^j$. The first (0-th) spike time is the immediate response to the stimulus at $t = t_0^j$. Now assume that for $m = 0, ..., k-1$ all neurons have emitted spikes at times $t_m^j = t_0^j + m\tau_0 + \mathcal{O}\left(\varepsilon\right)$, which is fulfilled for $k = 1$. Let $a_{j,i}^k = t_{k-1}^i + \tau_{j,i}$ denote the arrival time of the $k-1$-th action potential of neuron $i \in \mathrm{Pre}(\{j\})$ at neuron $j$. If $\varepsilon$ is sufficiently small we have for all $i_1, i_2 \in \mathrm{Pre}(\{j\})$:

$$|a_{j,i_1}^k - a_{j,i_2}^k| < \tau_e, \tag{10}$$

Hence, a spike of the $j$-th neuron is triggered by the last arrival at time

$$t_k^j = \max\left\{a_{j,i}^k\right\}_{i \in \mathrm{Pre}(k)} = \max\left\{t_{k-1}^i + \tau_{j,i}\right\}_{i \in \mathrm{Pre}(k)} = t_0^j + k\tau_0 + \mathcal{O}(\varepsilon). \tag{11}$$

Recursively, the value of $t_k^j$ can be expanded as

$$t_k^j = \max\left\{T\left(p\right) \mid p \in P_k\left(j\right)\right\}, \tag{12}$$

where $P_k\left(j\right)$ is the set which contains all paths of length $k$ ending in node $j$ and $T\left(p\right)$ is the total delay time of a path $p = (\ell_1, ..., \ell_k)$ plus the initial activation time $t_0^{p_1}$ of its starting point $p_1$, i.e.,

$$T\left(p\right) := t_0^{s(\ell_1)} + \sum_{j=1}^{k} \tau_{t(\ell_j), s(\ell_j)}, \tag{13}$$

where $s\left(\ell\right)$ and $t\left(\ell\right)$ denote the source and the target of a link $\ell$, e.g., $p_1 = s(\ell_1)$. For long paths, i.e. large $k$, the cycle $\bar{c}$ with the largest mean delay $\bar{\tau}$ will dominate the expressions for $t_k^j \sim \bar{\tau}k$. Therefore, we obtain

$$\min_n t_0^n + (k - 2N)\bar{\tau} + 2N \min_{m,n} \tau_{m,n} \leq t_k^j \leq \max_n t_0^n + (k - N)\bar{\tau} + 2N \max_{m,n} \tau_{m,n}. \tag{14}$$

In (14) the term $(k - 2N)\bar{\tau}$ is the delay time collected from the time spend in the cycle $\bar{c}$ and the terms $2N \min_{m,n} \tau_{m,n}$ and $2N \max_{m,n} \tau_{m,n}$ give generous bounds for the delays along the paths which are taken to reach $\bar{c}$ initially and to reach the target node after leaving $\bar{c}$. Using (14)

the difference of the $k$-th spikes of two neurons $i$ and $j$ can be estimated uniformly independent of $k$, $i$, and $j$ by

$$\left| t_k^j - t_k^i \right| \; \leq \max_n |t_k^n| - \min_n |t_k^n| \leq \; \max_{m,n} |t_0^m - t_0^n| + 2N \max_{m,n,l,p} |\tau_{m,n} - \tau_{l,p}| \leq \mathcal{O}(\delta) \quad (15)$$

This means, for sufficiently small perturbations of delay and stimulus times the system admits sustained synchronous activity. $\qquad\square$

**Proposition B.2.** *Consider a network with homogeneous in-degree $d_{\mathrm{in}} \equiv \nu$ and delay times $\tau_{i,j} \equiv \tau_0$ for all $j \in \mathrm{Pre}(\{i\})$ and assume that a sustained synchronous firing mode exists. If the sequence (5) becomes stationary at $\{1,...,N\}$, this mode is super-stable with respect to perturbed stimulation times, i.e. the synchronous spiking is achieved in finite time.*

*Proof.* With notations as in the previous proof we obtain for weakly perturbed stimulation times

$$t_k^j \;\; = \;\; \max\left\{ T\left(p\right) \mid p \in P_k\left(j\right) \right\} = \max_{m\in\mathrm{Pre}^k(\{j\})} t_0^m.$$

By stationarity of (5), for sufficiently large $k$, we have

$$\max_{m\in\mathrm{Pre}^k(\{j\})} t_0^m = \max_{1\leq n\leq N} t_0^n,$$

independent of $j$. Thus, the spiking becomes perfectly synchronous in finite time. $\qquad\square$

# C   Unique mode of sustained activity

In this section we consider a strongly connected network of coincidence detectors (1) with homogeneous delay $\tau_0$, in-degree equal to $\nu$ and the GCD of all cycles being one, i.e. there exist only loops of coprime lengths. Networks possessing the latter property are called *aperiodic* networks. We prove that the unique possible mode of sustained activity is synchronous spiking if the tolerance of the single detectors is sufficiently small.

Firstly, we give two counter-examples, where several sustained modes are possible. These examples should convince the reader that we need (i) an aperiodic network, (ii) a strongly connected network to guarantee the uniqueness of synchronous spiking. We remind once more, that if $\tau_0$ is large enough ($\tau_0 > 2\tau_r$) there may exist distinct synchronous solutions having shorter interspike intervals than $\tau_0$. We subsumed this coexistence under the claim of uniqueness. The more precise formulation is that synchronous spiking is the only possible mode of sustained activity.

**Example C.1.** (i) If the GCD of all cycles is $k > 1$, i.e., the network graph has period $k$, then there exists a partition $C_1, ..., C_k$ of the network such that the nodes are connected in a cyclic manner [62, Theorem 10.5.1]:

$$C_1 \to C_2 \to ... \to C_k \to C_1.$$

This means, all nodes from $C_j$ receive inputs exclusively from nodes in $C_{j-1}$ [see Fig. 9(c)]. Therefore, an initial, synchronous stimulation at $t = t_0$ of all nodes in $C_1$ will lead to a spike of all nodes in $C_2$ at time $t = t_0 + \tau_0$, of all nodes in $C_3$ at time $t = t_0 + 2\tau_0$ and so on in an indefinitely sustained cyclic activity, which is not globally synchronous. Cluster synchronization in delay-coupled dynamical systems with this kind of coupling structure have been studied in [63].

**Example C.2.** (ii) If the network is not strongly connected, a strongly connected component $C \subsetneq \mathcal{N}$ can be selected, which is a root in the associated acyclic graph, i.e., no links enter $C$. For each $k \in C$ we have $d_{\text{in}}(x_k)_{|C} = \nu$, therefore an initial, synchronous stimulation of $C$ will lead to a sustained synchronous activity in $C$ but this activity will take over the rest of the network only if no cycles exist on $\mathcal{N} \setminus C$. If such a cycle exists, some node $j \in \mathcal{N} \setminus C$ has $d_{\text{in}}(x)_{|\mathcal{N}\setminus C} > 0$ and $d_{\text{in}}(x)_{|C} = \nu - d_{\text{in}}(x)_{|\mathcal{N}\setminus C} < \nu$, which implies that it will never be excited by the synchronous spiking in $C$ if $\tau_e < \tau_0$. See Fig. 9(d) for a simple example of such a network.

From the study of the network shown in Fig. 3(a), and the existence of the wave-like solution [Fig. 3(c)] for this connection scheme, we already know that the tolerance time may not be too large, if only synchronous firing is desired. In the following proposition we give a bound in terms of $\tau_r$, which assures the uniqueness of the synchronous mode:

**Proposition C.3.** *If there exists $m_0 \in \mathbb{N}$ such that $\mathrm{Pre}^m(\{j\}) = \{1, ..., N\}$ for all $m \geq m_0$ and all $j \in \{1, ..., N\}$ and $d_{\text{in}}(x_j) \equiv \nu$. Then, for sufficiently small $\tau_e$ satisfying $0 < \tau_e < \tau_r < \tau_0$, the only possible mode of sustained activity is synchronous spiking.*

*Proof.* Assume that the dynamics displays an arbitrary mode of sustained activity. We have to show that for sufficiently small $\tau_e$ all nodes spike synchronously. To show that, choose an arbitrary node $j$ such that it fires at time $t = t_0$. We denote $t_{-n} := t_0 - n\tau_0$ and $T_{-n} := [t_{-n} - n\tau_e, t_{-n}]$. Since node $j$ fires at $t_0$, all its $\nu$ predecessors, $\mathrm{Pre}(\{j\})$, must have fired at least once within $T_{-1}$. Hence, their predecessors, $\mathrm{Pre}^2(\{j\})$, must have fired at least once in $T_{-2}$ and so on.

Within all the intervals $T_{-2m_0}, ..., T_{-m_0}$, all nodes fire at least once because $\mathrm{Pre}^m(\{j\}) = \{1, ..., N\}$, for $m = m_0, ..., 2m_0$, by assumption. Note that the width of all these intervals is bounded by $2m_0\tau_e$. Therefore, if we have

$$(2m_0 + 1)\tau_e < \tau_r, \tag{16}$$

each node fires exactly once in each of the intervals $T_{-m}$, $m = m_0, ..., 2m_0$, and each such firing in $T_{-m}$, for $m = m_0, ..., 2m_0 - 1$, is evoked exclusively by the $\nu$ firing events of its predecessors in $T_{-m-1}$, i.e., $x_k(t_{-m} - m\tau_e) \leq 1$ at the left boundary of $T_m$. Otherwise, at least on predecessor would have fired twice in $T_{-m-1}$, which we did just exclude. Recursively,

just as in the argument in the proof of Proposition [ref:stability-perturbed-times], we obtain

$$
\begin{aligned}
t^k_{-m} &= \max_{i \in \mathrm{Pre}(\{k\})} t^i_{-m-1} + \tau_0 \\
&= \max_{i \in \mathrm{Pre}^2(\{k\})} t^i_{-m-2} + 2\tau_0 \\
&\vdots \\
&= \max_{i \in \mathrm{Pre}^{2m_0-m}(\{k\})} t^i_{-2m_0} + (2m_0 - m)\tau_0.
\end{aligned}
$$

For $m = m_0$, this yields

$$
\begin{aligned}
t^k_{-m_0} &= \max_{i \in \mathrm{Pre}^{m_0}(\{k\})} t^i_{-2m_0} + m_0\tau_0 \\
&= \max_{1 \le i \le N} t^i_{-2m_0} + m_0\tau_0,
\end{aligned}
$$

independently of $k$. This means $t^k_{-m_0} = t_{-m_0}$ for all $1 \le k \le N$. We also conclude that all nodes fires exactly once within $(t_{-m_0} - \tau_r, t_{-m_0} + \tau_r)$. This implies, that no firing is evoked in the interval $(t_{-m_0} + \tau_0 - \tau_r, t_{-m_0} + \tau_0)$ and all nodes are in the resting state when the spikes from the synchronous firing at $t_{-m_0}$ arrives. Therefore, they fire synchronously at $t_{-m_0+1} = t_{-m_0} + \tau_0$ as well and likewise for all $t_m = t_{-m_0} + (m - m_0)\tau_0 = t_0 + m\tau_0$ with $m > m_0$. If there should be any firing events occurring between the synchronous firings at $t_m$ as determined before, they can be treated analogously to prove that they also form part of a sustained chain of synchronous firings. $\qquad\square$

*Remark* C.4. The number $m_0$ can be large, making the required bound (16) on $\tau_e$ quite strong. Even though the bound may not be optimal, the order $1/m_0$ appears to be necessary, if no further restrictions on $\tau_0$ are assumed. Indeed, for the network in Fig. 3(a), we have $m_0 = 6$, and there exists a non-synchronous sustained activity as long as $\tau_e > \tau_r/m_0$.

# D   A Lyapunov function for homogeneous degree networks

As a measure of activity in a network of coincidence detectors (1) we introduce the function

$$
V(t) := \sum_{j=1}^{N} (\max\{x_j(t^-), 1\} - 1) + \#\{\text{spikes in the wire}\} \in \mathbb{N}. \tag{17}
$$

Here, the term "$\#\{\text{spikes in the wire}\}$" refers to the number of emitted spikes which did not arrive at their destination, yet. More formally, it is given as

$$
\#\{\text{spikes in the wire}\} = \sum_{j} \#\{t^i_k \mid i \in P(j),\, 0 < t - t^i_k \le \tau_{j,i}\}.
$$

$V(t)$ is piecewise constant. The only moment at that $V(t)$ may grow is a spike event. If an element $x_j$ spikes at time $t = t_1$, $V$ changes by an amount $V(t_1^+) - V(t_1^-) = \nu - d_{\mathrm{out}}(x_j)$,

where $d_{\text{out}}(x_j)$ is the outdegree of $x_j$. (The value $c(x_j) := \nu - d_{\text{out}}(x_j)$ is called production capacity of $x_j$.) $V$ may as well decrease if $c(x_j) < 0$ for the spiking unit $x_j$. It can also decrease, if an excitation level at site $x_j$ reduces after a time $\tau_e$ has passed after the arrival of a presynaptic AP and no spike was emitted in the meantime or if an AP arrives while $x_j(t) = -1$. Notice that $V(t)$ is bounded if the refractory time doesn't vanish, i.e. $\tau_r > 0$. This is because a link with delay $\tau_{j,i}$ cannot contain more than $\tau_{j,i}/\tau_r + 1$ spikes. With help of $V$, sustained activity can be defined as a state in which $V(t) \neq 0$ for all times $t \geq t_0$.

Consider a network such that $d_{\text{out}}(x_j) \leq \nu$ for all $j$. Then $c(x_j) \leq 0$ and therefore, $V(t)$ is non-increasing. This means, it is a discrete Lyapunov function and on each attractor $V(t) \equiv V_0$ is constant. Obviously, the silent mode $V \equiv 0$, with $x_j \equiv 0$, is a fixed point of the system.

Given $d_{\text{out}}(x_j) \leq \nu$, there are some evident, necessary conditions for sustained activity. Firstly, each element which is involved in this activity by repeated spiking must have an outdegree $d_{\text{out}}(x_j) = \nu$. Otherwise, $V(t)$ would decrease each time when $x_j$ spikes. By the same reason, elements which receive an input of a participating element must participate in the sustained activity, too ("what comes in, must come out"). This restricts sustained activity to connected components with $d_{\text{out}}(x_j) = d_{\text{in}}(x_j) = \nu$ for all $x_j$ participating in the sustained activity. Moreover, it is necessary that there is no decrease of the excitation levels due to the expiration of excitation times and inputs may not arrive during refractory periods. That implies that at each unit, each time exactly $\nu$ spikes arrive collectively within a time intervals of length $\leq \tau_e$ which are separated by periods without inputs of length $> \tau_r$.

# E  The Hodgkin-Huxley neuron model

The Hodgkin-Huxley neuron model, which was used for the numerical results in Sec. 3, is given by the following set of equations:

$$C\dot{V}_j(t) = I - g_{Na}m^3h(V_j(t) - V_{Na}) - g_K n(V_j(t) - V_K) - g_l(V_j(t) - V_l) \tag{18}$$
$$- \kappa(V(t) - V_r)\sum_{j\in\text{Pre}(\{i\})} s_j(t - \tau_{i,j}) - \kappa^{\text{inh}}(V_j(t) - V_r^{\text{inh}})\sum_{j\in\text{Pre}(\{i\})} s_j^{\text{inh}}(t - \tau_{i,j}^{\text{inh}}),$$
$$\dot{m}_j(t) = \alpha_m(V_j(t))(1 - m_j(t)) - \beta_m(V_j(t))m_j(t),$$
$$\dot{h}_j(t) = \alpha_h(V_j(t))(1 - h_j(t)) - \beta_h(V_j(t))h_j(t),$$
$$\dot{n}_j(t) = \alpha_n(V_j(t))(1 - n_j(t)) - \beta_n(V_j(t))n_j(t),$$
$$\dot{s}_j(t) = 5(1 - s_j(t))/(1 + \exp(-V_j(t))) - s_j(t),$$
$$\dot{s}_j^{\text{inh}}(t) = (1 - s_j^{\text{inh}}(t))/(1 + \exp(-V_j(t))) - 0.3s_j^{\text{inh}}(t),$$

where $V_j(t)$ models the membrane potential of the $j$-th node, $\alpha_m(V) = (0.1V + 4)/(1 - \exp(-0.1V - 4))$, $\beta_m(V) = 4\exp((-V - 65)/18)$, $\alpha_h = 0.07\exp((-V - 65)/20)$, $\beta_h(V) = 1/(1 + \exp(-0.1V - 3.5))$, $\alpha_n(V) = (0.01V + 0.55)/(1 - \exp(-0.1V - 5.5))$, $\beta_n(V) = 0.125\exp((-V - 65)/80)$, $C = 1\mu\text{F/cm}^2$, $I = 0\mu\text{A/cm}^2$, $g_{Na} = 120\text{mS/cm}^2$, $V_{Na} = 50\text{mV}$, $g_K = 36\text{mS/cm}^2$, $V_K = -77\text{mV}$, $g_l = 0.3\text{mS/cm}^2$, $V_l = -54.5\text{mV}$, $V_r = 0\text{mV}$, $V_r^{\text{inh}} = -65\text{mV}$, $\kappa^{\text{inh}} = 0.1\text{mS/cm}^2$ and $\kappa = 0.05\text{mS/cm}^2$.

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