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The Difference Neuron—A new spiking Neuron Model

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Abstract

The previously proposed Neural Mode (J. Kanev, A. Koutsou, C. Christodoulou, K. Obermayer; 2016; *Neural Computation*, 28(10):2091-2128) quantifies to what extent spiking neurons use temporal integration or coincidence detection to calculate a response to their stimulus. While the Neural Mode is easy to measure, parameterising a neuron model to show a certain level of coincidence detection or integration is not straightforward. We propose a new spiking neuron model – the Difference Neuron – that integrates or detects coincidences according to a predefined value of the Neural Mode. The Difference Neuron is a simple model without internal states, receiving one or several trains of spike times. It can be configured to detect simple coincidences, gaps or more complex patterns covering separate stimulus spike trains. It can exhibit spike bursting, and it covers areas of mathematical operation a biological neuron does not - it can spike without stimulus, it can operate purely on inhibition, and it can show inhibition and coincidence detection combinations that are unavailable to other neuron models. Sparsely connected networks of Difference Neurons can show different levels of regular and irregular synchronisation, depending on the Neural Mode of their neurons. We explore several single-neuron examples and investigate the neuron’s behaviour. Because this new model does not include differential equations describing membrane potentials or ion concentrations, but computes its response spike times from simple time comparisons, we believe the Difference Neuron will simplify investigations into dynamics of spiking neurons and networks, and into spike patterns and the mechanisms of the neural code.

Keywords: Spiking neuron model Spiking neural network Difference Neuron Neural Code Interval Code

1 Introduction

Neurons are stimulated by synaptic input caused by a succession of voltage spikes and they respond to this stimulus at different time scales, in a deterministic and robust way. Typically a change in the neuron’s response reflects a change in its stimulus (Mainen and Sejnowski 1995). If a neuron responds to changes of the overall stimulus rate without reflecting the timing of single spikes, we

say that the neuron temporally integrates. If a neuron reacts to the timing of just a few close stimulus spikes, we say that the neuron detects coincidences (König et al. 1996). Coincidence detection and synchrony play an important role in the way information is accessed and processed in the brain (Abeles 1982; Cariani 2001; Benda et al. 2006; Chen et al. 2013; Metzen et al. 2020; Azeredo Da Silveira and Rieke 2021; Susin and Destexhe 2021; von der Malsburg 2021; Mabil

et al. 2024; Stoll et al. 2024; Huo et al. 2025) and shape the way neurons learn (Christodoulou and Cleanthous 2011; Cleanthous and Christodoulou 2012; Frémaux and Gerstner 2016; Masquelier 2018). It has been shown that the role of a neuron – coincidence detector or integrator – is relevant for stimulus encoding and for operation within a neural population (Joris et al. 1998; Roy and Alloway 2001; Bostner et al. 2020; Azghadi et al. 2021). Neurons act in a continuum between coincidence detection and integration (König et al. 1996; Kisley and Gerstein 1999; Rudolph and Destexhe 2003; Koutsou et al. 2012; Zavou et al. 2017), or could use either of those modes simultaneously on different parts of their stimulus (Brette 2015; Kanev et al. 2016).

Investigating the level of coincidence detection independently from other neural features is important in understanding neural coding (Grewé et al. 2017), however, setting up neuron models to spike in a predefined way is not straightforward (Bell et al. 1995; Arcas et al. 2002; Fortuna and Buscarino 2023). This is because there are several biological mechanisms that shape the sensitivity to different frequency ranges, like synaptic and dendritic influence on firing threshold (Pant et al. 2003; Azouz and Gray 2000; Fortuna and Buscarino 2023), a combination of membrane time constant and firing threshold (Kempter et al. 1998a, 1999; Fortuna and Buscarino 2023), the shape of the postsynaptic response function, the number of synapses, and the statistics of the stimulus (Kempter et al. 1998b).

To better understand neural information processing, it makes sense to view a neuron as a computational machine. Biological parameters like reversal potentials, the number of synaptic release sites, membrane potential values, or time constants influence the computational performance of a neuron very indirectly. Under the assumption that the computational mode of operation of a neuron describes its behaviour in a much more fundamental and direct way, a neuron model without secondary parameters is needed, where this “operational mode” can be set directly (Mel

2000). Such a model would help to investigate neuron dynamics in different time scales.

A recently proposed measure called the Neural Mode quantifies whether a neuron is doing coincidence detection or integration, and the related Neural Drive measures whether its stimulus inhibits or excites the neuron (Kanev et al. 2016). Both measures describe the relationship of a set of stimulus spike times to a set of response spike times. As soon as these are available – *in vivo* or *in vitro* from live recordings, or *in silico* using simulation results from any popular neuron model – the Neural Mode can be obtained easily. However, using current neuron models to predict the Neural Mode analytically, or even finding a parameter set that makes a neuron operate in one or the other mode, is difficult.

In this paper we propose, explain, and demonstrate a new spiking neuron model – the Difference Neuron – that allows to pre-determine the amount of integration or coincidence detection, that can cover all possible regions of Neural Modes and Drives, that is as simple as possible, and that should reflect the spiking behaviour of existing biologically inspired random walk models. The Difference Neuron reacts to time differences between stimulus spikes and thus implements a difference code. It is a non-biological, mathematical neuron model. It can be configured to show bursting, and in addition to coincidence detection and integration the possible range of its response behaviours covers extreme cases that a biological neuron could not show – it can spike without stimulus, it can operate purely on inhibition, and it can show inhibition and coincidence detection combinations that are unavailable to biological neurons or common neuron models, like gap detection or inhibition by stimulus gaps. Such a neuron can replace traditional models, making it easier to investigate the mechanisms of spike-timing neural code and the underlying rules of neural information processing.

In the Model section we explain the building blocks and the mechanics that make up the Difference Neuron. In the Methods section we briefly explain details of the numerical simulations we

have conducted. In the Results section we demonstrate the effect of the model parameters on the neuron’s response behaviour. We continue with networks of Difference Neurons that can be configured to show regular or irregular synchronisation, we then compare a Difference Neuron to a leaky Integrate-and-Fire Neuron. We compare networks of Difference Neurons with networks of Integrate-and-Fire Neurons. In the Discussion section we put our findings into context and suggest a few ideas about future steps.

2 The Model

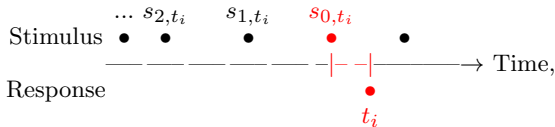
2.1 The Neural Mode and Drive

The measures of Neural Drive and Neural Mode were introduced in (Kanev et al. 2016) and express whether a neuron is excited or inhibited by its stimulus and whether it is detecting coincidences or is integrating. The Neural Mode and Drive characterise the relation between an existing set of stimulus spike times and a set of response spike times. They can be calculated for model neurons as well as for recordings of biological neurons.

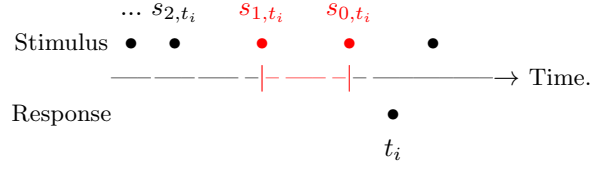
A neuron receives an ordered set $S = \{s_0 < s_1 < \dots\}$ of stimulus spike times and computes an ordered set $T = \{t_0 < t_1 < \dots < t_K\}$ of K response spike times, where the s_i are times when the neuron receives a stimulus spike and the t_i are times when the neuron emits a response spike. Let s_{0,t_i} be the time of the stimulus spike closest before the response spike at t_i ,

$$s_{0,t_i} = \max\{s \in S | s < t_i\},$$

and let s_{n,t_i} be the n th stimulus spike before the response at t_i . Consider the distance between the last stimulus spike and a following response, $t_i - s_{0,t_i}$,



and the distance between the last two pre-response spikes, $s_{0,t_i} - s_{1,t_i}$,



Their averages over all K responses of the neuron,

$$r_0 = \frac{1}{K} \sum_{i=0}^K (t_i - s_{0,t_i}) \quad \text{and} \quad (1)$$

$$r_1 = \frac{1}{K} \sum_{i=0}^K (s_{0,t_i} - s_{1,t_i}), \quad (2)$$

indicate the average response delay after the last stimulus spike (r_0), and the mean inter-spike interval preceding a response (r_1).

Let us call the mean distance between any random point in time and the nearest preceding stimulus spike r_0^* . Normalising r_0 by r_0^* and scaling to stretch from -1.0 to 1.0 results in the Neural Drive R_D :

$$R_D = 2^{1 - \frac{r_0}{r_0^*}} - 1. \quad (3)$$

The Neural Drive expresses whether a neuron is excited or inhibited by its stimulus. If a neuron responds immediately after a stimulus, the stimulus excites it and R_D will be near 1.0. If a neuron responds when the last stimulus has been some time ago and there hasn’t been any stimulus since then, the arriving stimulus suppresses the neural response for a fixed time period. In this case the stimulus inhibits the neural response and R_D will be near -1.0.

Let us call the unconditional mean stimulus inter-spike interval r_1^* . Normalising r_1 by r_1^* and scaling it to stretch from -1.0 to 1.0 constitutes the Neural Mode R_M :

$$R_M = 2^{1 - \frac{r_1}{r_1^*}} - 1. \quad (4)$$

The Neural Mode shows whether a neuron integrates or detects coincidences. If a neuron

responds on average to pairs of spikes that are much closer together than expected, it detects coincidences, and R_M will be near 1.0. If a neuron responds mainly to pairs of spikes that are an average distance apart, it integrates, and R_M will be near 0.0. If a neuron responds on average to pairs of spikes that are a lot wider apart than expected, it detects gaps in the stimulus. Figure 1 provides an overview of the different regions in the $R_{M,D}$ plane. (See the original publication (Kanev et al. 2016) for more details.)

2.2 Difference Detectors

“Difference Detectors” are the building blocks of the Difference Neuron, operating in the Neural-Mode-and-Drive plane of the stimulus.

The Neural Mode and Drive are averages created in retrospect, after measuring a large number K of stimulus-spike-pair-and-response triplets. In contrast, a Difference Detector responds to a local, “real-time” estimate of the Neural Mode and Drive where only the last stimulus spike pair is considered and $K = 1$. Using the current time instead of the time stamp of an observed response t_i , the distance to the latest stimulus and the width of the latest stimulus spike pair are constantly monitored. To distinguish this single-time Mode and Drive from the averaged measure $R_{M,D}$ we index the symbols R_M and R_D with the current time t :

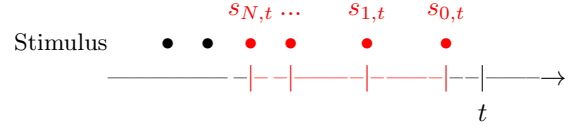
$$R_{D,t} = 2^{1-d} - 1, \quad d = \frac{t - s_{0,t}}{r_0^*},$$

$$R_{M,t} = 2^{1-m} - 1, \quad m = \frac{s_{0,t} - s_{1,t}}{r_1^*},$$

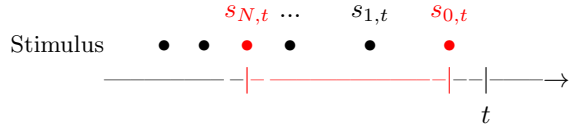
where $s_{0,t}$ is the most recent stimulus spike time, $s_{1,t}$ is the stimulus spike before $s_{0,t}$, and r_0^* and r_1^* are expectation values (see previous section 2.1 and later section 2.4). As before, $R_{D,t}$ and $R_{M,t}$ denote single values for the online Drive and Mode respectively, while $R_{MD,t}$ denotes the corresponding tuple of the online forms of the Neural Mode and Drive at the current time t .

Using a single-response-spike form of the Neural Mode and Drive and constantly measuring the stimulus against the current time is necessary for

the Difference Detector to react to single stimulus spikes in real time. However, forming the Neural Mode from single stimulus spikes can result in an unstable, erratic response behaviour, in particular for high-rate stimuli. To compensate this disadvantage, Difference Detectors may use a sum of N pre-response stimulus inter-spike intervals $\sum_{k=1}^N (s_{k+1} - s_k)$ to calculate the Neural Mode.



Simplifying to $s_0 - s_N$



results in

$$R_{M,t}^N = 2^{1-m} - 1, \quad m = \frac{s_{0,t} - s_{N,t}}{r_N^*}, \quad (5)$$

where r_N^* is the unconditional expected width of N consecutive inter-spike intervals. The parameter N determines the number of spikes that constitute any coincidences the detector reacts to. If $N = 1$, one pair of stimulus spikes forms a coincidence, if $N > 1$ the detector considers larger stimulus spike groups.

A Difference Detector has a rectangular Sensitive Zone in the $R_{M,D}$ plane. If the current $R_{MD,t}^N$ value is within this Sensitive Zone, a detector’s state $\delta = 1$, otherwise $\delta = 0$. An overview of a Difference Detector’s parameters is given in Table 1.

In the $R_{M,D}$ plane, the most recent stimulus spike pair (or volley of N spikes, if $N > 1$) is represented by one point. The width of the spike pair determines the Neural Mode value (Y axis), the time since its occurrence determines the value of the Neural Drive (X axis). As time passes, this point travels to the left, staying at the same height (Neural Mode value). When the next stimulus spike appears, it forms the last spike of a new pair

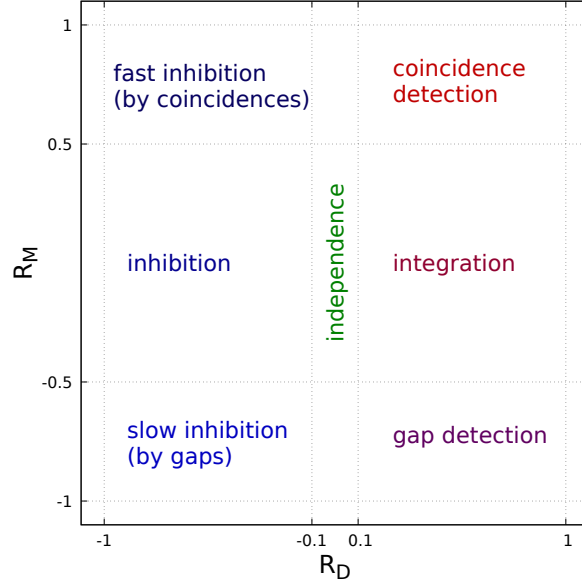


Fig. 1: The $R_{M,D}$ plane of the Neural Mode and Drive.

The two-dimensional measure of Neural Mode (coincidence detection/integration) and Neural Drive (excitation/inhibition) shows the average neural response with respect to the inter-spike interval size of the last stimulus spike pair and the stimulus-response latency. The original publication defined different regions: Coincidence detection – on average the neuron responds shortly after stimulus spike pairs with short inter-spike intervals (spike coincidences). Integration – on average the neuron responds shortly after a stimulus spike, independent of the stimulus spike pair time distance. Gap detection – on average the neuron responds directly after long inter-spike intervals (stimulus gaps). Independence – the neuron’s average response is indistinguishable from a spike train that is independent of the stimulus. Fast inhibition – on average the neuron responds after pairs of near-coincident spikes followed by silence. Inhibition – independent of the stimulus frequency, the neuron responds only if there hasn’t been any stimulus for some time. Slow inhibition – the neuron responds on average after long inter-spike intervals followed by silence. (See (Kanev et al. 2016) for more details.)

Symbol	Range	Unit	Meaning
d^+, d^-	$[-1, 1]$		Upper and lower borders of the Sensitive Zone’s drive.
m^+, m^-	$[-1, 1]$		Upper and lower borders of the Sensitive Zone’s mode.
w	$[0, 1]$		The weight of the detector.
δ	$\{0, 1\}$		The current state of the detector.
N	$\mathbb{N}$		The amount of stimulus spikes used for capturing the Neural Mode R_M^N .
r_0^*	$\mathbb{R}^+$	s	The expected distance between any random time and the latest stimulus before (for static detectors).
r_N^*	$\mathbb{R}^+$	s	The expected time interval of N consecutive stimulus spikes (for static detectors).
M	$\mathbb{N}$		The amount of stimulus spikes to estimate r_0^* and r_N^* (for dynamic detectors).

Table 1: Parameters of a Difference Detector.

(or volley) that is again represented by a point starting its path on the right border of the $R_{M,D}$ plane, at $R_D = 1.0$, causing the previous point to disappear. Its height is related to the R_D value

of the previous point. Figure 2 shows an example. The red numbers 1-9 in the top plot show the evolution of measurements for the spike train plotted in red in the bottom plot.

With one excitatory Sensitive Zone of non-zero width a neuron would keep firing at infinite rate, as long as the stimulus value remained inside the Sensitive Zone. To prevent this, feedback Difference Detectors are used – Difference Detectors that monitor the neuron’s response instead of its stimulus. Apart from being connected to a different input source, a feedback Difference Detector is a standard Difference Detector, using the same parameters (see Table 1). Typically a receptive feedback zone would be inhibitory - allowing responses only a certain time after the previous response. When time is discretized, this is an effective way to make sure a response spike lasts exactly one time step.

2.3 The static Difference Neuron

Much like a synapse, each Difference Detector is connected to a stimulus source, and feedback Difference Detectors may be connected to the neuron’s output. Each detector has a single rectangular Sensitive Zone in the $R_{M,D}$ plane. Detectors are indexed using a running i . A detector compares the intervals in the stimulus spike train with fixed values for r_0^* and r_N^* . If the currently measured $R_{MD,t}$ value is inside its Sensitive Zone, a detector’s state $\delta = 1$, otherwise $\delta = 0$. The neuron fires a response Δ as long as the weighted sum of detector states exceeds 1.0:

$$\Delta = \begin{cases} 1, & \text{if } \sum_i w_i \delta_i \geq 1.0 \\ 0, & \text{if } \sum_i w_i \delta_i < 1.0 \end{cases} \quad (6)$$

See Table 1 for an overview of model parameters.

The configuration of Sensitive Zones can be displayed graphically. Since the neuron reacts to time differences between consecutive stimulus spikes and thus implements a difference code, we chose the term “Difference Neuron”, despite one earlier alternative use of the term (Seligson et al. 1992).

At least one inhibitory feedback Difference Detector is needed to transform the plateau shaped activation into a time stamp of a response spike. The weights of all Difference Detectors must be chosen such that without the negative feedback

Difference Detector, the neuron cannot fire. With time being binned, a neural response $\Delta = 1$ in one time bin will cause a measurement of $R_{D,t} = 0$ at the negative feedback Difference Detector in the next time bin. If the feedback Difference Detector has its Sensitive Zone set up to be inhibitory, that value of $R_{D,t} = 0$ will be outside its Sensitive Zone, setting the neuron’s $\Delta = 0$ in that time bin. This way an inhibitory feedback Difference Detector ensures response spikes of one time bin width, even for arbitrarily small time bins.

The first values of a Difference Detector’s $R_{MD,t}$, at the beginning of a numerical simulation when no stimulus spikes have been detected yet, are defined to be zero.

This completes the model. A Difference Neuron has several Difference Detectors, each connected to a spike source. Each Difference Detector has a Sensitive Zone, an $R_{MD,t}$ value of its connected stimulus at the current time, and a detector activation state. The neuron fires a response Δ when the weighted sum of detector states exceeds 1.0.

The example displayed in Figure 2 illustrates the standard operation of a Difference Neuron with two Difference Detectors, both with expected spike intervals of $r^* = 5$ (arbitrary units), and weights of $w = 0.6$ (both detectors must be active for the neuron to emit a spike). One is a feedback Difference Detector, and one is a stimulus Difference Detector. Time starts with the feedback Difference Detector being active ($\delta = 1$) and the stimulus Difference Detector being inactive ($\delta = 0$). At $t = 1$ two coincident (0.5 time units apart) stimulus spikes arrive (bottom plot, red). The stimulus Difference Detector measures at a high R_M , and at $R_D = 1$ (top plot, red “1”). At $t = 2$ a time of 1 has passed. The stimulus Difference Detector measures a lower R_D . The measurement is now inside the Sensitive Zone (red square) and the stimulus Difference Detector becomes active ($\delta = 1$; middle plot, red, just before 2). With both detectors active, the neuron is active ($\Delta = 1$; bottom plot, green, at 2). The response detector measures this response with $R_D = 1$ (top

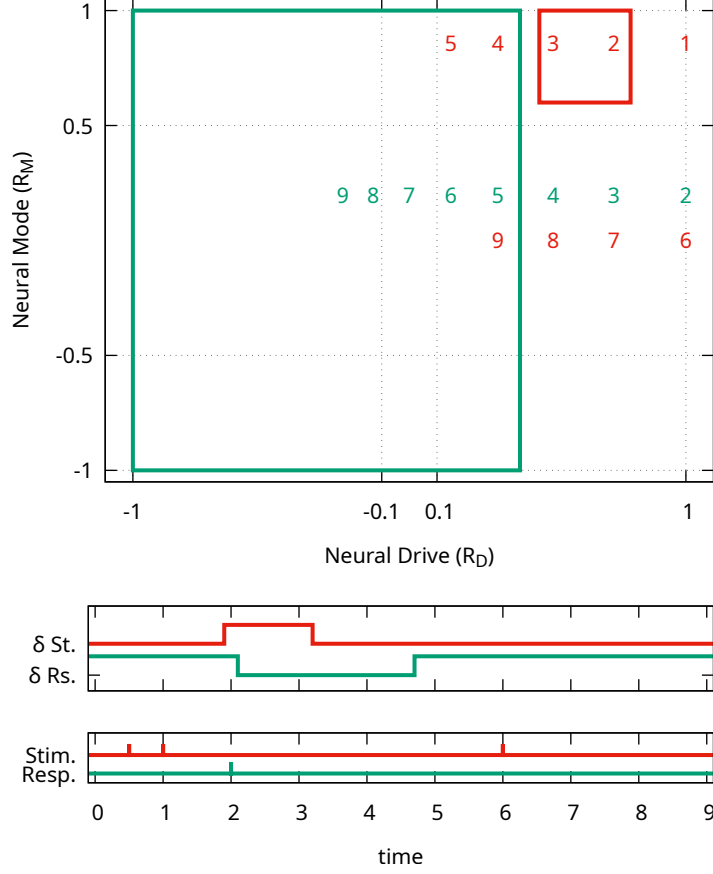


Fig. 2: Stimulus, difference calculation, and response.

A neuron with one stimulus Difference Detector δ_s and one response feedback Difference Detector δ_r , both with expected inter-spike interval of 5 (arbitrary units), during operation. **Top plot:** Measurements in $R_{M,D}$ space by the stimulus Difference Detector (red) and the response detector (green). Large squares mark the stimulus Difference Detector's Sensitive Zone (red) and the response detector's Sensitive Zone (green). Red numbers 1-9 show the location in $R_{M,D}$ space of measurements by the stimulus Difference Detector at time points 1-9. Green numbers 2-9 show locations of the response detectors measurements at times 2-9. **Middle plot:** Activation δ of the stimulus (red, labelled " δ St.") and response (green, labelled " δ Rs.") Difference Detectors over time. **Bottom plot:** Stimulus (red, labelled "Stim.") and response (green, labelled "Resp.") spikes over time. For a explanation see section 2.3.

plot, green "2"), outside its zone, and the detector state becomes $\delta = 0$ (middle plot, green, just after 2). With only one detector active, the neuron becomes inactive ($\Delta = 0$; bottom plot, green, just after 2). At $t = 3$ the distance to the last spike has increased for both detectors. At $t = 4$ the stimulus Difference Detector measure is outside the Sensitive Zone (top plot, red "4"), the detector becomes inactive ($\delta = 0$; middle plot, red, between 3 and 4). At $t = 5$ the time since the last response is large enough to be measured inside the Sensitive

Zone (top plot, green "5"), the response detector becomes active again. The refractory period is over. At $t = 6$ a stimulus spike arrives, exactly 5 after the previous stimulus spike. This equals the stimulus Difference Detector's expected distance r_0^*, s , hence the stimulus Difference Detector measures at $R_D = 1$ and $R_M = 0$). At $t = 7$ to 9 time increases, and measurements for both detectors move left, with increasing drive R_D .

Although a Difference Neuron could be simulated using asynchronous dynamic time steps, in most practical scenarios a fixed time step size

dt would be used. The step size should be chosen such that even close single stimulus spikes are resolved and do not end up in the same time bin. Our tests showed that the time step dt of a numerical simulation should be one or two orders of magnitude lower than the average stimulus inter-spike interval.

2.4 The dynamic Difference Neuron

The expectation values r_0^* and r_N^* , used to normalise the Neural Mode and Drive, can either be fixed model parameters, or dynamically estimated at run-time.

For a dynamic estimation of r_N^* – the expected time span made up by N stimulus spike pairs – a Difference Detector can continuously keep track of the last M stimulus spikes with M being sufficiently large, and then divide by M to get an estimate of r_1^*

$$r_1^* \approx \frac{s_{0,t} - s_{M,t}}{M}. \quad (7)$$

Assuming that $r_N^* \approx Nr_1^*$ we obtain

$$r_N^* \approx N \frac{s_{0,t} - s_{M,t}}{M} \approx Nr_1^* \quad (8)$$

(again using the notation $s_{0,t}$ for the latest stimulus spike time before t), at any time t . Note that r_1^* is the first moment of the inter-stimulus interval series.

For a dynamic estimation of r_0^* – the expected distance between the latest stimulus and the current time – a Difference Detector could look at the time interval between a long ago stimulus spike $s_{M,t}$ and the most recent stimulus spike $s_{0,t}$ at the current time t , measure the time difference between any point τ inside that interval and the latest stimulus spike $s_{0,\tau}$ preceding it, integrate this difference over time and divide it by the total interval size:

$$r_0^* \approx \frac{1}{s_{0,t} - s_{M,t}} \int_{s_{0,t}}^{s_{M,t}} (\tau - s_{0,\tau}) d\tau.$$

This would be computationally expensive. However, if we integrate piece-wise between each stimulus spike pair and add the result at the end, then replace all integrals with their solution,

$$\begin{aligned} r_0^* &\approx \frac{1}{s_{0,t} - s_{M,t}} \sum_{i=0}^{M-1} \int_{s_{i+1,t}}^{s_{i,t}} \tau d\tau \\ &= \frac{1}{s_{0,t} - s_{M,t}} \sum_{i=0}^M \frac{1}{2} (s_{i,t} - s_{i+1,t})^2, \end{aligned}$$

and replace the total length $s_{0,t} - s_{M,t}$ with Mr_1^* (according to (7)), we obtain

$$r_0^* \approx \frac{1}{2} \frac{\sum_{i=0}^{M-1} (s_{i,t} - s_{i+1,t})^2}{Mr_1^*}. \quad (9)$$

This is half the ratio of the second and the first moment of the stimulus inter-spike interval (see Table 1 for an overview of all parameters).

In the following we call neurons with static detectors using fixed values “static neurons”, and neurons with dynamic detectors using the online estimations of r_N^* and r_0^* (cf. 8, 9) “dynamic neurons”. In this work, the only Difference Detectors that are dynamic are stimulus detectors. All feedback Difference Detectors are static.

3 Methods

All numerical simulations in this paper were implemented in C++, using the NeuroLab¹ framework. To showcase the response of the Difference Neuron to specific stimuli we conducted several numerical simulations with a time resolution of $dt = 0.1$ ms (see Table C2 for parameter details of Difference Neurons with a single stimulus source and Table C3 for parameter details of Difference Neurons with two stimulus sources.) To demonstrate the effect of different positions of the stimulus zone on the neuron’s mean, CV, Neural Mode, and Drive we averaged the neuron’s response across various parameter ranges. Each

¹NeuroLab is an OpenSource C++ class library for numerical simulation and analysis of stochastic processes in neuroscience, available online since 2005 and continually evolving. Source code and documentation can be downloaded from *GitHub* at <https://github.com/jkanev/neurolab>.

of the resulting plots contains 200 data points where each data point is an average of 2000.0 simulated seconds. Before recording, 10.0 simulated seconds were run to allow the dynamic neuron to adapt its stimulus rate estimate. See Table C1 for parameter details of the averaged parameter explorations.

To investigate the behaviour of the Difference Neuron in a sparsely connected network, we set up a network consisting of 250 neurons. Neurons were inter-connected with a connection probability of 0.1. Pre-synaptic response spikes from connected neurons and the external stimulus were combined before feeding them into the Difference Detectors. Rate expectations for all zones were set to 10 Hz, all zones had a multiplicity of $N = 1$. After exploring three static scenarios running for 20 seconds each, we performed a parameter exploration in ten consecutive five-second intervals. After each five-second interval the network was reset (all Difference Detectors were set to their initial state and their list of past spike times was cleared) and the position of the stimulus zone changed. For this setup we recorded a spike scatter plot, total network activity, mean network activity over the five-second interval, and the network synchrony during the five-second interval. See Table C4 for a parameter overview. The amount of network synchrony was estimated using an approximation of the Synchronisation Measure $\chi(n)$ proposed by (Golomb et al. 1992; Golomb and Rinzel 1993; Golomb et al. 1994; Ginzburg and Sompolinsky 1994), see Appendix Appendix B. for calculation details. The value of $\chi(n)$ ranges from 0 (not synchronised at all) to 1 (fully synchronised).

To compare the behaviour of a Difference Neuron to a leaky Integrate-and-Fire Neuron (LIF), we used Simulated Annealing to find an optimal parameter fit of a Difference Neuron to a pre-defined LIF Neuron. We modelled an LIF Neuron (the trainer) according to the equation

$$dV_t = \sum_i w_i(v_i - V_t)dG_t^i, \quad (10)$$

where w_i are weights, v_i are reversal potentials and dG_t^i are derivatives of stochastic processes.

In one setup we used one excitatory conductance with $v_E = 10$ mV, $w_E = 0.2$, $dG_t^E = dN_t$, where dN_t is the derivate of the Poisson counting process, and one leak conductance with $v_L = -50$ mV, $w_L = \frac{1}{\tau} = \frac{1}{20.0\text{ms}}$, and time $dG_t^E = dt$:

$$dV_t = w_E(v_E - V_t)dN_t^E + w_L(v_L - V_t)dt.$$

In a second setup we included an additional inhibitory conductance with a reversal potential of $v_I = -70$ mV, excitatory (N^E) and inhibitory (N^I) Poisson stimuli being independent:

$$dV_t = w_E(v_E - V_t)dN_t^E + w_I(v_I - V_t)dN_t^I + w_L(v_L - V_t)dt.$$

Whenever V_t crossed a threshold V_θ , a spike of height of 30 mV was emitted, and V_t was reset to $v_R = -70$ mV. The connection strengths w were chosen such that biologically plausible stimuli from a large number of pre-synaptic neurons, using a realistic threshold value, produce realistic response rates. For details of the fitting procedure, see Appendix A. After fitting the static Difference Neurons to the LIF, we compared the LIF Neuron to two Difference Neurons, one with a static expected stimulus rate and one with an adaptive stimulus rate. We use the parameters from the fitting algorithm: One excitatory zone, connected to excitatory stimulus, with $R_D = (0.9, 1.0)$, $R_M = (0.430, 1.0)$, $N = 8$, and one feedback zone, connected to the neuron's response, using with $R_D = (-1.0, 0.75)$, $R_M = (-1.0, 1.0)$, $N = 1$. One neuron had an expected stimulus rate of 500 Hz, the other estimated the expected rate dynamically at run time. Weights for both zones were set to $w = 0.6$ – both zones are required for the neuron to fire. The excitatory zones of both Difference Neurons and the LIF Neuron shared the same stimulus, a Poisson sampled excitatory stimulus with varying rate $50\text{ Hz} \leq \lambda_E \leq 950\text{ Hz}$. Simulations were executed with a step size of $dt = 0.01$ ms. Both the Difference Neurons and the LIF Neurons received the same stimulus and were simulated using the

same time step size. The plots in Figure 17 were created from 200 runs, each lasting 500.0 simulated seconds, preceded by 10.0 seconds that were not recorded, so the dynamic neuron could adapt the stimulus rate estimate. Table C6 shows an overview of parameters, including results from the fitting procedure.

To investigate the behaviour of sparsely connected networks of Difference Neurons, we set up up three networks consisting of 100 neurons each. One network consisted of static Difference Neurons, a second network of dynamic Difference Neurons, and a third network of LIF Neurons. Neurons in each network were interconnected with a connection probability of 0.1 and received stimuli of different frequencies (350 Hz, 450 Hz, 800 Hz). All three networks were identically connected, i.e., respective neurons in different networks had identical connections and identical random input. The LIF Neurons and the Difference Neurons were set up with parameters from the simulated annealing fit. Pre-synaptic response spikes from connected neurons and the external stimulus were combined before applying the Difference Neurons’ Difference Detector or the Integrate-and-Fire Neurons’ conductances. A detailed parameter overview is given in Table C7. We explored the network behaviour across a range of stimulus rates, measuring the response mean (all responses added, and divided by stimulation time length), the CV (standard deviation obtained in the same way and divided by the mean), and the network synchronisation (see equation B3). For this we conducted 3000 simulations starting at a stimulus rate of 350 Hz, increasing the stimulus by 0.05 Hz between two simulations, ending at 500 Hz. Each point in the resulting plot (figure 20) was obtained from networks with a different random connection structure. Since the inter-neural connection structure has a much greater effect on the network’s response than the slightly changing stimulus rate, the original plot was very noisy. To smooth the plot, at each f the average $\bar{x}(f)$ of adjacent simulation results $x(f)$ was computed as $\bar{x}(f) = x(f - 0.9Hz) + x(f - 0.8Hz) + \dots + x(f + 0.9Hz)$.

4 Results

4.1 Neural Mode

The model we consider has two Sensitive Zones – the Sensitive Zone of the Difference Detector connected to the stimulus (we will call this zone “stimulus zone” for brevity) and the Sensitive Zone of the Difference Detector connected to the neuron’s own response (“feedback zone”). How does the Neural Mode position of a Sensitive Zone affect the spiking behaviour of a Difference Neuron? Figure 3a shows the Sensitive Zones of a Difference Neuron with one feedback (green) and one stimulus zone (red) at a high Neural Mode value. Responses by that neuron to a stimulus spike train generated by a Poisson process are shown in Figure 3b. Figure 3c shows a Difference Neuron with a stimulus zone at a low Neural Mode value but otherwise equal model parameters. Responses by that neuron to a random stimulus spike train are shown in Figure 3d. While responses of the neuron with its stimulus zone at high values of R_M occur after stimulus spikes that form close pairs, response spikes of the neuron with its stimulus zone at a low R_M occur after the first stimulus spike after a long pause in the stimulus spike train. A Difference Detector becomes active when the $R_{M,t}$ component of the current measurement is between the top and bottom borders of the detector’s Sensitive Zone. Reversing equation (4) to

$$\frac{r_1}{r_1^*} = 1 - \log_2(R_M + 1)$$

shows that an R_M value of $m^- = 0.5$ for the lower border would correspond to a normalised width of a stimulus spike pair of 41.5% of the stimulus mean r^* , while an upper border value of $m^+ = 1.0$ would correspond to a normalised distance of 0. The zone in Figure 3a is sensitive to stimulus spike intervals between 0 and 41.5% of r^* . For a value of $r_1^* = 100$ ms (see Table C2) this results in a neuron being sensitive to inter-spike intervals in its stimulus of $0 \text{ ms} \leq r_1 < 41.5 \text{ ms}$. Equally, the stimulus zone in Figure 3c is sensitive to stimulus inter-spike intervals of $220 \text{ ms} \leq r_1 < \infty$. This means

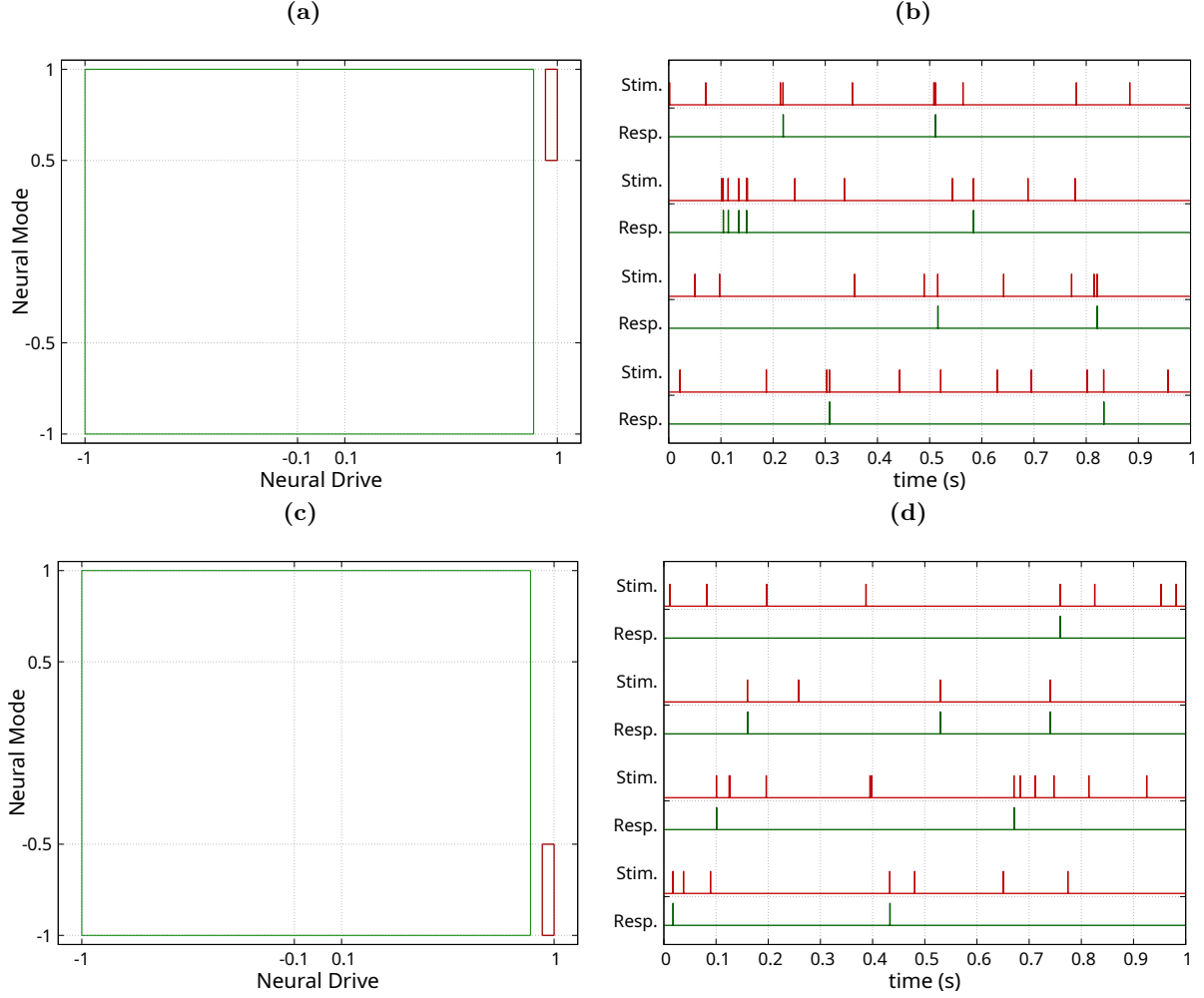


Fig. 3: The Neural Mode of the Stimulus Zone influences coincidence vs. gap detection.

Sensitive zones and activity of two Difference Neurons. (a): Red – Sensitive Zone of Difference Detector connected to the stimulus spike train, zone set to coincidence detection and positive drive. Green – Sensitive Zone of Difference Detector connected to the neural response (feedback), creating a refractory period. (b): Response spike trains (green) in response to the stimulus (red). Four traces of one second simulated length each show examples of the same parameter configuration. (c): Red – coincidence detector connected to stimulus; zone set to gap detection and positive drive. Green – coincidence detector connected to neural response (feedback), creating a refractory period. (d): Response spike trains (green) in response to stimulus (red) for the Difference Neuron shown in (c). Four traces of one second simulated length each show examples of the same parameter configuration. For explanation, see section 4.1. For parameters see Table C2.

the Neural Mode position of the stimulus zone determines whether the neuron responds to dense stimulus spike groups, to sparse spike groups, or is indifferent to the stimulus inter-spike interval.

How do the response properties Neural Mode, Drive, mean, and variance of a Difference Neuron change when the Neural Mode position of its stimulus zone changes? Does this differ between a dynamic and a static neuron? Figure 4 shows the neuron’s response properties to different R_M

positions of the stimulus zone. Two Difference Neurons with one feedback and one stimulus zone were simulated, one neuron using a dynamic estimation for r^* of the stimulus and the other using a fixed value. While not changing the zone’s size nor any other parameters of the Difference Neuron, the stimulus zone was moved continuously from low R_M (gap detection) to high R_M (coincidence detection). Figure 4a shows the zone positions and sizes for both neurons at the beginning and at the

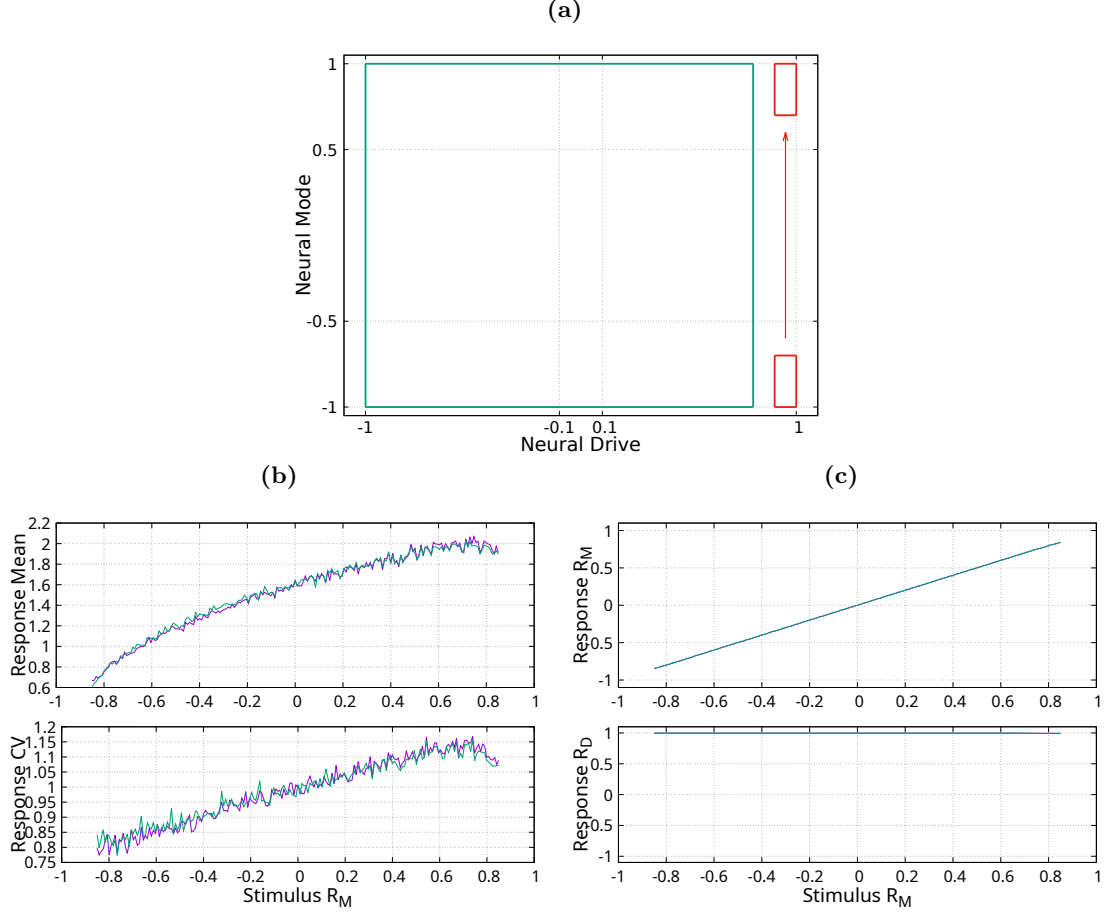


Fig. 4: Response properties as a function of the Neural Mode of the Stimulus Zone.

Sensitive Zones and activity of two Difference Neurons, exploring different Neural Mode positions of an excitatory stimulus zone. (a) Sensitive Zones of the Difference Detectors. Green - feedback zone, creating a fixed refractory period. Red - excitatory zone, at the beginning of the parameter exploration in the gap detection region of the Neural Mode (bottom right), at the end in the coincidence detection area (top right). (b) Mean spike rate (top) and coefficient of variation (bottom) of a static (purple) and a dynamic (green) Difference Neuron, plotted against the center of the Neural Mode of the excitatory Sensitive Zone. (c) Neural Mode (top) and Neural Drive (bottom) estimated from the response spike train of the static (purple) and the dynamic (green) Difference Neuron, plotted against the changing Neural Mode center of the excitatory Sensitive Zone. The purple and green curves coincide exactly. For explanation see section 4.1. For parameters see Table C1.

end of this exploration. The neuron with dynamic stimulus rate estimation responds in the same way as the neuron with the static stimulus rate setting. During the linear transition of the stimulus zone, the neuron's Neural Mode rises linearly, while the Neural Drive stays at the highest value (Figure 4c). The mean and coefficient of variation of the response spike train change in a non-linear way, being highest when the Sensitive Zone is in the coincidence detection area of the Neural Mode (Figure 4b). At the end, when the zone reaches the top of the Neural Mode continuum, response

mean and CV slightly decrease again. The Neural Mode of the neuron is a direct result of the Neural Mode position of the stimulus zone. The feedback zone has no influence on the Neural Mode. The relation of the zones' positions and the response mean and CV is more complex. A stimulus zone that does not span the complete height of the $R_{M,D}$ -plane would be active for a sub-set of all possible stimulus inter-spike intervals. For a neuron that responds instantly, a succession of response inter-spike intervals is computed from

the train of stimulus inter-spike intervals by merging each stimulus inter-spike interval that does not match the zone borders with the subsequent interval. If that (now merged) subsequent inter-spike interval does not fit the zone criteria either, its successor will be merged to the interval too, and so forth. If a Sensitive Zone accepts coincidences but rejects gaps, short inter-spike intervals will trigger a response, while gaps will be merged with the next interval. This extends each gap by a random value (the mean of which is the global ISI mean), while each coincidence remains unchanged. However, if a Sensitive Zone accepts gaps but rejects coincidences, short inter-spike intervals will be extended, on average by the mean ISI, while long intervals remain unchanged. Assuming the same amount of intervals to be merged in either case, and assuming their summed length to be the same, merging coincidence intervals with their successors (in the case of gap detection) will result in a much lower average inter-spike interval than merging gaps with their successors. That is why moving a Sensitive Zone from gap detection to coincidence detection without changing the zone's size increases the response rate.

A similar argument explains the increase in the response CV when the Sensitive Zone is moved from gap detection to coincidence detection. In the case of coincidence detection the response train consists of small inter-spike intervals (unchanged from the stimulus), while the large intervals from the stimulus have been enlarged further (by merging with the next interval). This increases the variance. In the case of gap detection the response train consists of the large intervals from the stimulus, while the short intervals from the stimulus have been enlarged. This results in a lower variance. This effect is slightly diminished again if the Difference Neuron's response intervals get near the rejection area of its feedback zone. In that case more stimulus coincidence intervals are merged into larger response intervals again, causing a decrease in the response rate and variance (Figure 4b, right). The dynamic and the static neuron behave the

same way because the stimulus rate was kept constant. The dynamically estimated stimulus rate is noisy, but the difference to the static value has an expectation of zero.

This means, when moving the stimulus zone, the measured Neural Mode and Drive of the Difference Neuron move with the stimulus zone. A neuron can be configured to operate at a certain Neural Mode at any point between the extremes of gap detection and coincidence detection by simply placing a Sensitive Zone in the corresponding area of the Neural Mode continuum.

4.2 Neural Drive

How does the Neural Drive position of a Sensitive Zone affect the spiking behaviour of a Difference Neuron? Figure 5a shows one large feedback zone (green), and one stimulus zone (red) spanning the whole Neural Mode range with an upper Neural Drive border of $d^+ = 1.0$. The response to a stimulus spike train generated by a Poisson process is shown in Figure 5b. Figure 5c shows a similar setup, but with a stimulus zone at a lower Neural Drive of $d^+ = 0.5$, the response by that neuron to a random stimulus spike train is shown in Figure 5d. Finally, a setup with a stimulus zone at $d^+ = 0$ is shown in Figure 5e, the response is shown in Figure 5f. The neuron with an upper stimulus drive border at 1.0 responds immediately after each stimulus spike (Figure 5b). For $d^+ = 0.5$ (Figure 5c) there is a response delay of 24 milliseconds (Figure 5d) and not every stimulus spike triggers a response. Last, Figures 5e and 5f show a delay of 100 milliseconds with even fewer stimulus spikes eliciting responses.

If a Sensitive Zone spans the whole range of the Neural Mode, its activity depends on the timing of the last stimulus spike only, not on the interval size. The upper Drive border d^+ is the first border a measurement crosses in $R_{M,D}$ space when moving from right to left (see also Figure 2 and explanatory text). If that border is at 1.0 (Figure 5a), the Difference Detector becomes active immediately at the time of the stimulus spike. Provided the feedback zone does not block fast responses, each stimulus spike triggers a response (Figure

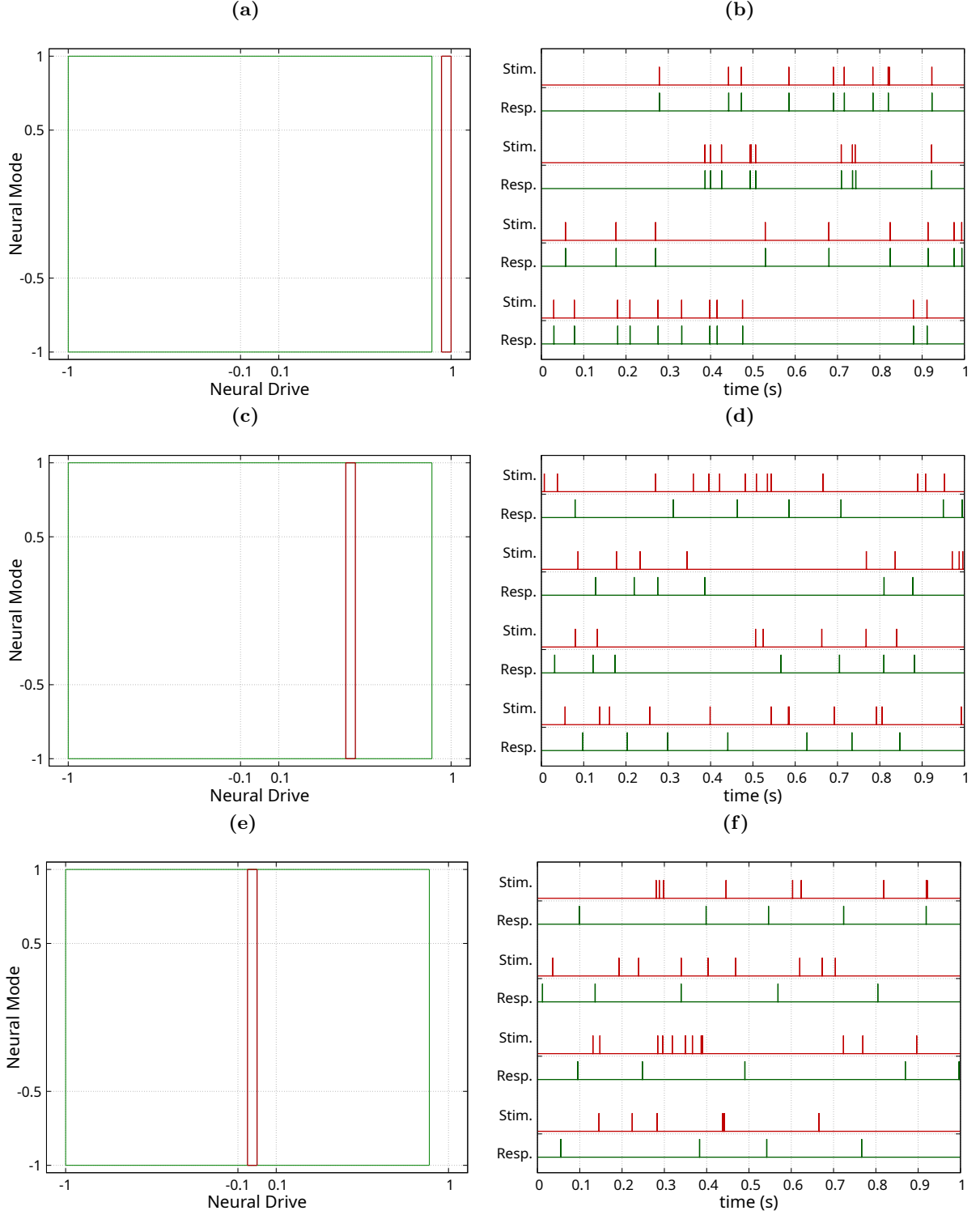


Fig. 5: The Neural Drive of the Stimulus Zone determines response delay.

Sensitive Zones and activity of three Difference Neurons with different Response Delays. **(a)**, **(c)**, **(e)**: Sensitive zones for each Difference Neuron. Red – Difference Detectors connected to stimulus spike train, green – Difference Detectors connected to the neural response spike train (feedback). **(b)**, **(d)**, **(f)**: Spike traces, showing four traces of one second simulated length for each Difference Neuron. Red traces – stimulus spike trains, green traces – response spike trains. For explanation see section 4.2. For parameters see Table C2.

5b). With the Drive border further to the left, at $d^+ = 0.5$, the detector becomes active when the measurement has travelled a distance of 0.5 to the left, i.e., after 41.5 ms for the chosen parameters (Figure 5c), and the neuron responds with a delay (Figure 5d). Importantly, delays reduce the response frequency, because a response can only occur if the next stimulus spike appears after the delay interval. Since the detector’s activity is always calculated with respect to the latest stimulus spike, a new stimulus spike that appears before the delay time is over will be measured at $R_D = 0$ again. Effectively only stimulus spike intervals that are larger than the delay time trigger a response. Figure 5f shows the result of an upper drive border of $d^+ = 0$ (fields in Figure 5e). The neuron responds only to stimulus intervals that are larger than the mean inter-spike interval. The stimulus has an inhibitory effect, i.e., the neuron only responds when the stimulus frequency is sufficiently low.

This means the Neural Drive position of a Sensitive Zone determines the delay of the neural response. Larger delays decrease the response rate. For values $R_D < 0$ of the Neural Drive, the Difference Detector is more often inactive than it is active, causing the stimulus to have an inhibitory effect.

What happens to the response mean and coefficient of variation of a Difference Neuron when the Neural Drive position of the stimulus zone changes? Does this differ between a dynamic and a static neuron? Figure 6 shows the neuron’s response properties to different R_D positions of the stimulus zone. Two Difference Neurons with a feedback zone and a stimulus zone were simulated, one neuron using a dynamic estimation for r^* of the stimulus and the other using a fixed value. The stimulus zones spanned the whole Neural Mode range. Without changing the zone’s size, the stimulus zone’s position was moved continuously from a low Neural Drive (inhibition) to a high Neural Drive (excitation). Figure 6a shows the zone positions and sizes for both neurons at the beginning and at the end of the exploration.

While moving the stimulus zone across the Neural Drive range, the measured Neural Drive of the neural response rises linearly while the Neural Mode stays constant at $R_M \approx 0$ (Figure 6c). The response mean is rising with R_D in an almost linear way, with the static neuron’s mean showing prominent jumps at certain R_D values when the dynamic neuron’s mean shows gentle bumps only. The response CV first drops when moving from strong ($R_D \approx -1.0$) to weak inhibition ($R_D \approx 0$), but slightly rises again to a value of 1.0 for full excitation without a delay ($R_D = 1.0$). As the stimulus zone is not selective to a specific range of the Neural Mode, the neural response depends only on the time passed since the last stimulus spike. With a drive < 0 a response spike will only be emitted during stimulus gaps that are larger than the average stimulus interval, with a drive ≈ 1 response spikes occur after every single stimulus spike (if the refractory period permits). Increasing the drive of the stimulus zone (moving it right) thus increases the response rate. The response Drive and Mode of a Difference Neuron with a single stimulus zone will always be within the borders of that zone, as confirmed by the measurement in Figure 6c. The discontinuities in the mean and CV in Figure 6b are caused by bursting. When Sensitive Zones are in different areas of the $R_{M,D}$ space, identical widths translate to exponentially different time intervals. The range of stimulus spike time delays that can trigger a response is much larger when the Sensitive Zone is near -1.0 than when it is near 1.0. Depending on the maximum response frequency allowed by the feedback zone, larger stimulus zones can allow several response spikes in a row (more about spike bursts in section 4 Results—Bursting). While the absolute width of the stimulus zone decreases, fewer and fewer spikes make up one burst. Each time the response burst consists of one spike fewer, the response mean changes discontinuously, as does the CV. This is because responses with bursts have a much higher CV than non-burst responses. In our example, above $R_D = 0$ only single response spikes occur. In the dynamic neuron, where the expected stimulus rate is estimated

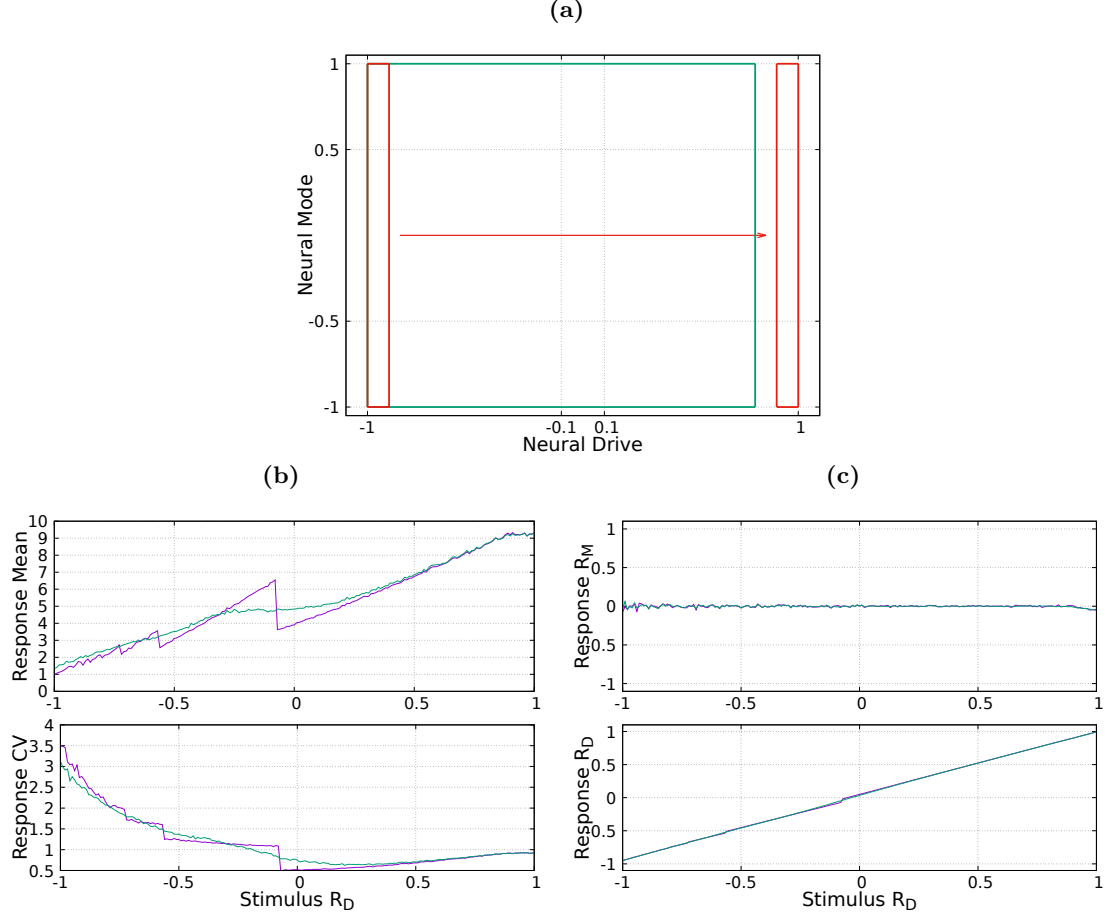


Fig. 6: Response properties as a function of the Neural Drive of the Stimulus Zone.

Sensitive Zones and activity of two Difference Neurons, exploring different positions of an excitatory stimulus zone. **(a)** Sensitive Zones of the Difference Detectors. Green – feedback zone, creating a fixed refractory period. Red – excitatory zone; at the beginning of the exploration in the inhibitory part of the Neural Drive continuum (left), at the end in the excitatory part (arrow, and right). **(b)** Mean (top) and CV (bottom) of the static Difference Neuron (purple) and the dynamic Difference Neuron (green) against the changing Neural Drive center of the Sensitive Zone. **(c)** Neural Mode (top) and Neural Drive (bottom) of the static Difference Neuron (purple) and the dynamic Difference Neuron (green) while the Neural Drive increases. The purple and the green curves coincide exactly. For explanation see section 4.2. For parameters see Table C1.

dynamically, no discontinuities appear at specific values of R_D . Because the normalisation factor r^* is a continuously updated estimate, the precise length of the stimulus interval that activates the Difference Detector keeps slightly changing. This results in smoother changes in the mean and CV of the dynamic neuron (green curves in Figures 6b and 6c) as opposed to the discontinuities in the purple curves.

This means, when moving the stimulus zone, the Neural Drive of the Difference Neuron moves with the zone. A neuron can be configured to operate at a certain neural Drive at any point between

the extremes of strong inhibition and strong excitation by simply placing a Sensitive Zone in the corresponding area of the Neural Drive continuum. The relation of response rate and of response CV to the Neural Drive position of the stimulus zone is more complex, in particular when bursting is involved. In general, higher Drive means higher response rate.

4.3 Bursting

Difference Neurons can respond with spike bursts. How do the shapes of stimulus and feedback zones

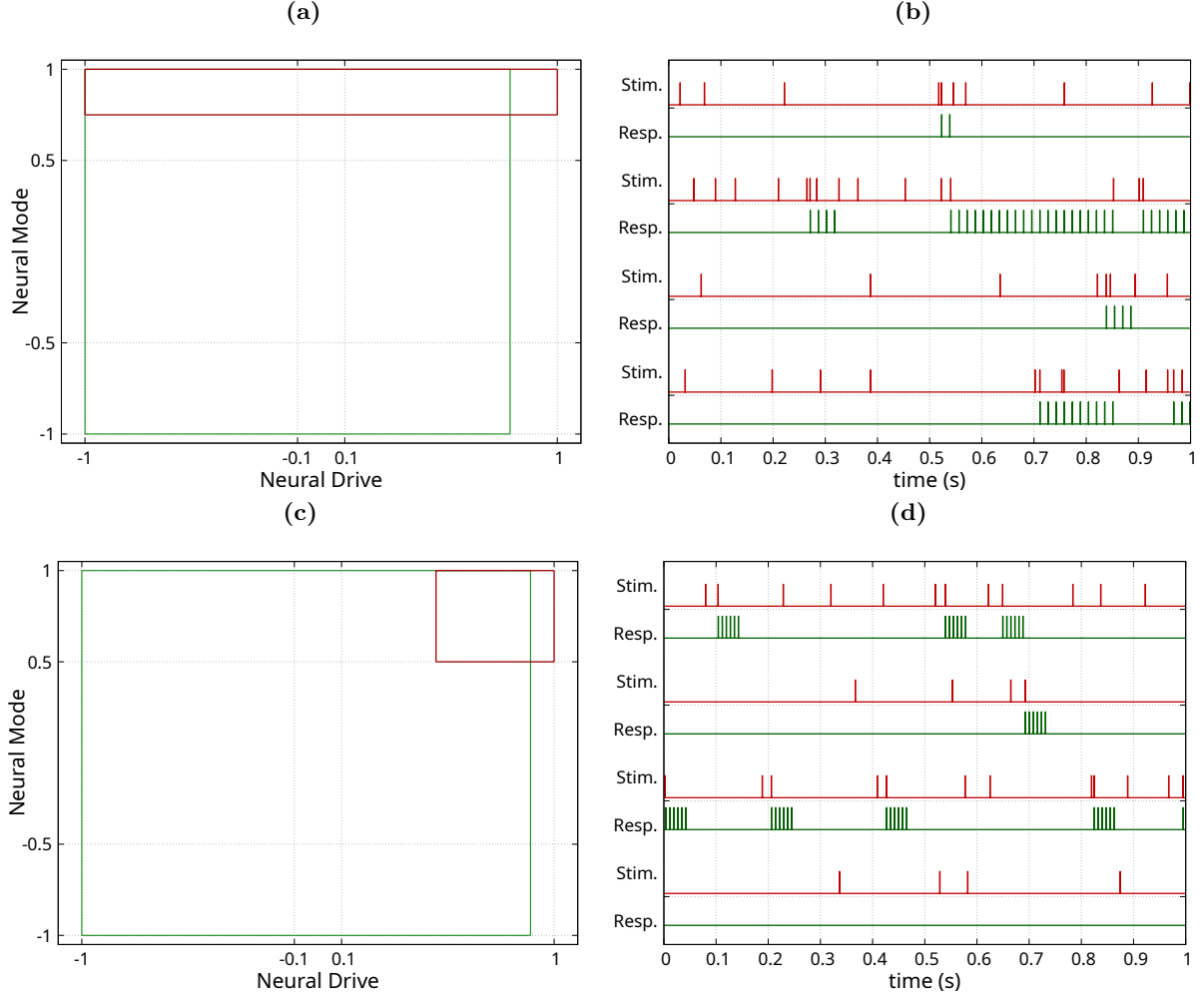


Fig. 7: The width of the Sensitive Zone influences spike bursting.

Sensitive Zones and activity of two Difference Neurons showing spike bursting. (a), (c): Red – Sensitive Zones of Difference Detectors connected to the neuron’s stimulus (stimulus zones). Stimulus zones create active response intervals after the stimulus. Green – Sensitive Zones of Difference Detectors connected to the neural response (feedback zones). Feedback zones create fixed refractory periods. (b), (d): Red traces – stimulus spikes, green traces – response spikes. For explanation see section 4.3. For parameters see Table C2.

influence the spike bursts? Figure 7 shows results for two neurons that are configured to produce bursts of spikes. In one setup the stimulus zone spans the whole width of the Neural Drive (Figure 7a), resulting spike trains in Figure 7b. In the other, the stimulus zone is narrower in the R_D dimension (Figure 7c), resulting spike trains in Figure 7d. If the stimulus zone spans the whole width of the Neural Drive, bursts will continue until a gap in the stimulus occurs. If the stimulus zone is narrower in the R_D dimension, the length of a spike burst is limited. Independently, a

higher value of the maximum drive border of the feedback zone (right drive border) causes a lower inner-burst frequency than a smaller value. After the neuron has fired a response spike, the feedback zone prevents further responses for a fixed time. If that time is over and the stimulus Difference Detector is still active, another response spike is generated and the refractory period starts again. This continues until the stimulus Difference Detector becomes inactive, either because the next stimulus spike has caused an $R_{MD,t}$ value outside the Sensitive Zone, or because the current

measurement has left the Sensitive Zone while moving to the left with time. The inner-burst frequency is determined by the refractory period of the neuron – as long as all other Difference Detectors are active the neuron will produce a response spike as soon as the $R_{D,t}$ value of its previous response crosses the right (d^+) border into its feedback zone. Larger values of d^+ mean higher inner-spike frequencies while lower values of d^+ mean lower frequencies (compare the right border of the green zones in Figures 7a and 7c, as well as the spike frequencies inside each spike burst in Figures 7b and 7d). This means, if the absolute width of the stimulus zone is larger than the gap between the right border of the feedback zone and 1.0, a neuron shows spike bursts. The maximal length of a burst depends on the width of the stimulus zone, the inner-burst frequency depends on the d^+ border of the feedback zone.

4.4 Multiplicity

The multiplicity N (cf. Table 1) determines how many spikes are measured to find the average Neural Mode. How do different values of N affect the neuron’s response behaviour? Figure 8 shows three neurons with identical Sensitive Zones – a large feedback zone and a stimulus zone in the coincidence detection area of the $R_{M,D}$ plane – but with different values of N . Figure 8a shows the Sensitive Zones. The neurons respond to stimuli that contain single spikes as well as spike clusters. Figures 8b, 8c, 8d show the stimulus spike trains (red) and the response spike trains (green) of Difference Neurons with stimulus zones of $M = 1, 3$, and 5. The stimulus consists of single spike and larger clusters. In figure 8b there is a response to each close (< 42 ms) stimulus spike pair. The response in 8c (green) shows fewer response spikes, here only after at least four close by stimulus spikes. Figure 8d shows even fewer response spikes, here only after clusters of at least six close stimulus spikes. With a multiplicity of $N = 1$ the Neural Mode is measured using two stimulus spikes. If a neuron is configured to respond to coincidences like in Figure 8a, it will respond to each stimulus spike pair that is shorter than a given

time interval (here: 42 ms, Figure 8b). If the multiplicity is increased to $N = 3$, the neuron does not respond unless four consecutive stimulus spikes arrive in a given time interval (here: less than 120 ms, Figure 8c). If the multiplicity is increased to $N = 5$, the neuron responds only if at least six stimulus spikes arrive within a given time interval (here: 210 ms, Figure 8d). This means, using the multiplicity parameter N , Difference Neurons can be made sensitive to incoming bursts of a certain size N while ignoring smaller spike groups. For this, r_N^* has to be larger than a pre-synaptic spike burst of N spikes, or $1/r_N^*$ has to be equal or smaller than the inner-burst frequency divided by N .

4.5 Neuron with two or more Sensitive Zones

The Difference Neuron is able to detect a large variety of stimulus features if more than one Sensitive Zone is used. For the sake of brevity we limit the introduction to two Difference Detectors connected to two separate stimulus sources and one feedback detector, their weights chosen such that all detectors have to be active for the neuron to spike. What happens if coincidence detection is combined with an inhibitory stimulus? Figure 9 shows three neurons with excitatory and inhibitory sensitive zones. One neuron 9b has distinctively excitatory and an inhibitory zone. Excitatory (red) and inhibitory (blue) stimulus spikes occur randomly. The neuron responds directly after excitatory coincidences but only if inhibitory spikes had occurred more than a certain minimum delay time ago. The neuron in figure (d) receives two regular spike trains with similar but not identical frequencies. The neuron responds when both stimuli appear simultaneously. The neuron in figure (f) receives the same two regular spike trains, but responds when a red stimulus spike appears shortly after a blue stimulus spike. The neuron fires a response spike whenever a spike coincidence in the excitatory stimulus is less than 15.2% of its expected width (here less than 76 ms apart) and the latest inhibitory stimulus spike

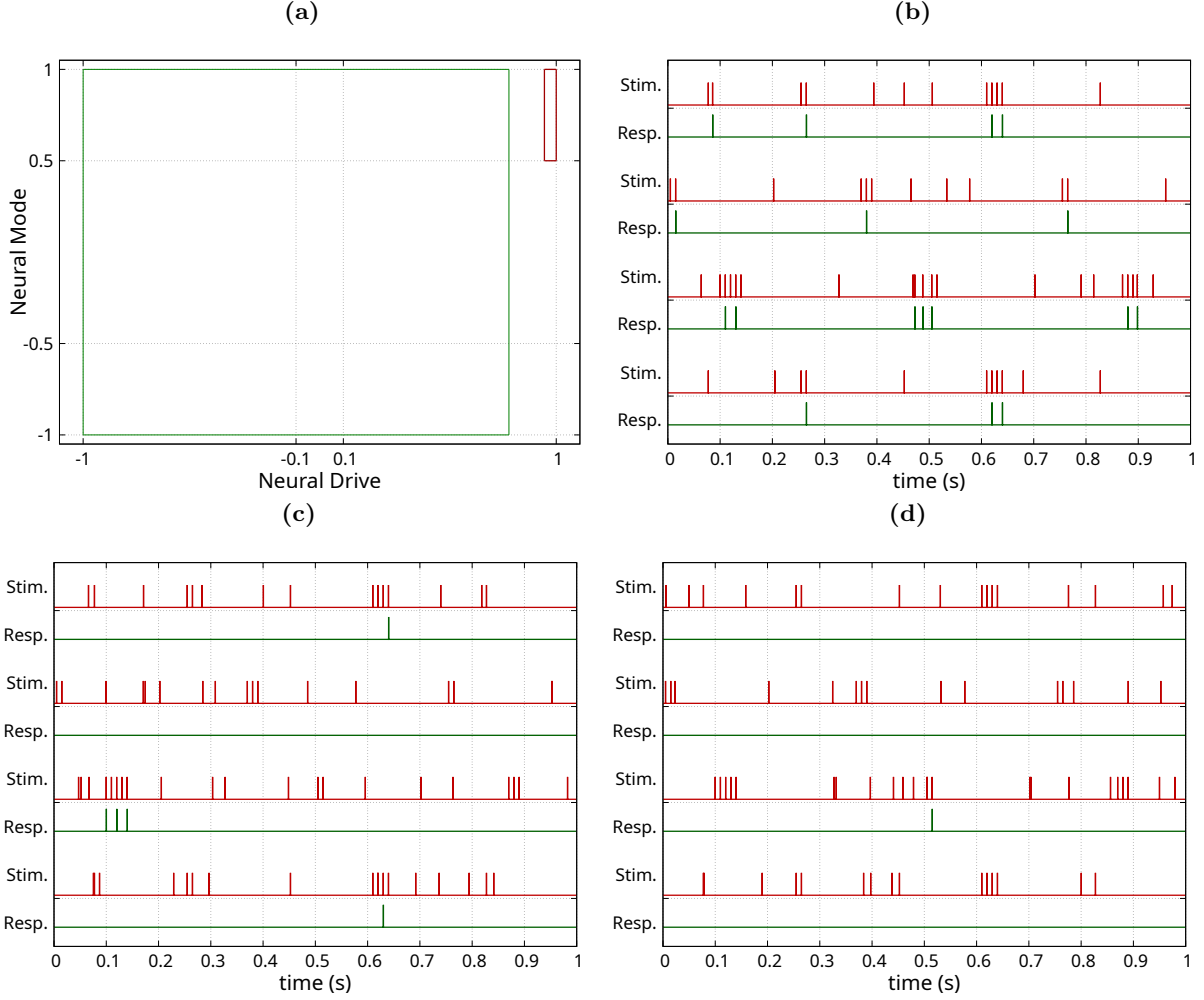


Fig. 8: Role of the multiplicity parameter.

Sensitive Zones and activity of three Difference Neurons with different multiplicity parameter values. (a): Sensitive Zones for all three Difference Neurons. Green – Difference Detector connected to neural response (feedback), creating a fixed refractory period. Red – Difference Detectors connected to stimulus. (b): Multiplicity $N = 1$ (stimulus pairs). (c): Multiplicity $N = 3$ (stimulus spike groups of four). (d): Multiplicity $N = 5$ (stimulus spike groups of six). For explanation see section 4.4. For parameters see Table C2.

is at least 11.5% longer ago than expected (here more than 115 ms in the past, Figure 9b). A stimulus is “excitatory” if the neuron emits a response immediately after its arrival. This means the Neural Drive must be large. The opposite is true for inhibition, a stimulus is “inhibitory” if the neuron is silent during its presence and emits a response only when the last stimulus spike is some time ago. This means the Neural Drive must be small. This means, with multiple Sensitive Zones and a threshold that is set such that all their activity is needed for the neuron to fire, their effects

add. Coincidences in the excitatory stimulus will trigger a response, unless there is an inhibitory stimulus present at the same time.

What happens if the two Sensitive Zones overlap? Figure 9c shows a Difference Neuron with two Sensitive Zones spanning the full height of the $R_{M,D}$ plane. Both zones are exactly on top of each other. Figure 9d shows the response to regular stimuli that have slightly different frequencies. The neuron responds when spikes from both stimuli appear close to each other, otherwise it remains silent. The Sensitive Zones span the full

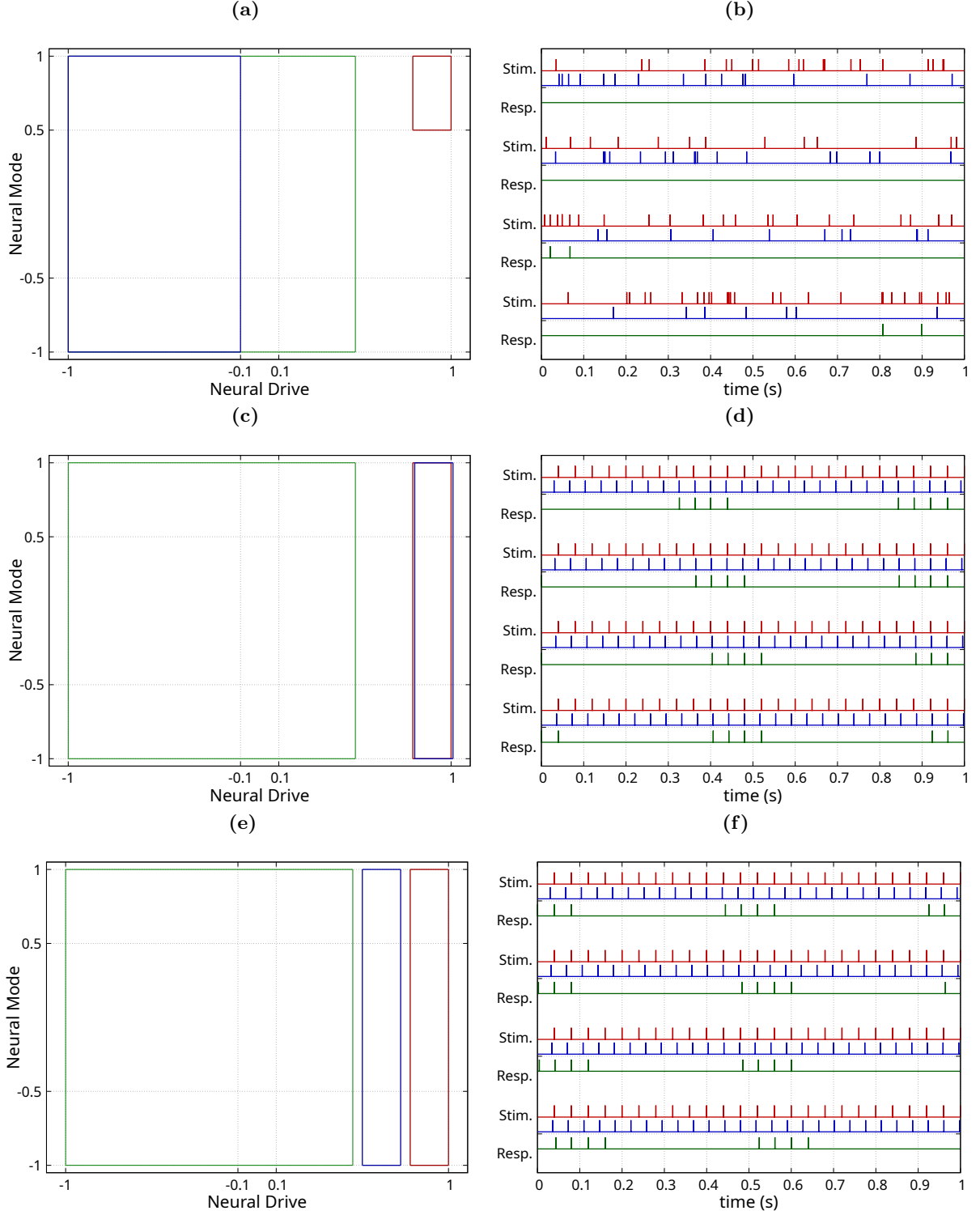


Fig. 9: Different neurons with two Stimulus Zones.

Sensitive Zones and activity of three Difference Neurons receiving input from two separate stimulus sources. **(a)**: Neuron with an excitatory (red) and an inhibitory (blue) zone. **(b)**: Random excitatory (red) and inhibitory stimulus spikes (blue), and neural response spikes (green). **(c)**: Neuron with two identical excitatory stimulus zones (red and blue). **(d)**: Regular stimulus spike trains of different frequency (red and blue) and neural responses (green). **(e)**: Neuron with two staggered excitatory stimulus zones (red and blue). **(f)**: Stimuli (red and blue) and neural responses (green). For explanation see section 4.5. For detailed parameter values see Table C3.

height of the $R_{M,D}$ plane, making them insensitive to the ISI of incoming spike pairs. Both zones are exactly on top of each other, so the neuron responds only when both Difference Detectors see a stimulus at the same time. The width of the zone ($0.8 \leq R_D \leq 1.0$) determines the tolerance up to which the two spikes are still considered coincident – here at the most 15% of the expected width, in this case 15 milliseconds. This means, while a single Sensitive Zone can detect coincidences within one stimulus spike train, using two Sensitive Zones on top of each other a neuron can detect coincidences between separate stimulus spike trains.

What happens if the two Sensitive Zones are placed next to each other? Figure 9e shows a similar setup as before, but one of the Sensitive Zones is shifted to the left and the zones do not overlap any more. Figure 9f shows the neural response to two regular stimulus spike trains with slightly different frequencies. A response spike is generated when a spike in one stimulus spike train (red curve) appears after a spike in the other stimulus spike train (blue), where the Neural Drive difference between the two Sensitive Zones determines the required delay (Figure 9e). The neuron responds at the time of the second spike. This means, more complex temporal relations can be created by placing multiple Sensitive Zones into different parts of the $R_{M,D}$ plane.

4.6 Networks of Difference Neurons

How does a network of pure coincidence detectors behave? Figure 10 shows Sensitive Zones of Difference Neurons in such a network (Figure 10a), a scatter plot of network activity (Figure 10b, top, red), and the total network activity over time (bottom, black). The scatter plot shows synchronised events separated by intervals of silence of about 10 ms – 500 ms. The sharp lines are synchronous responses of roughly half the network’s neurons (Figure 10b bottom, black, shows the exact distribution). Occasional single responses of single neurons occur. Due to the sparse connections, the network is largely driven by stimulus. Neurons react fast to coincidences

in their stimulus, adding more coincidences, taking other neurons with them. Bound to their hard refractory period, after a synchronised response neurons become silent synchronously. There is some jitter in the range of milliseconds due to the delay mentioned above. Being stimulus driven also means that the irregularity at which synchronised responses occur is caused by the irregularity of coincidences in the stimulus. This means, a sparsely connected network of Difference Neurons configured as coincidence detectors can exhibit sharp synchronised irregular responses.

How does a network of pure coincidence detectors behave if the fixed minimum inter-response interval is chosen randomly for different neurons in the network? Figure 11a shows the Sensitive Zones of the neurons in such a network, the differently sized feedback zones of all neurons are overlaid in the same diagram. The minimum Neural Drive, the minimum, and the maximum Neural Mode are identical for all neurons. The maximum Neural Drive (right border) is randomly chosen from a constant distribution between -0.5 and 0.5. Figure 11b shows a scatter plot of network activity (top panel) and the total network activity over time (bottom panel). The scatter plot shows synchronous responses that cover between 60 and 140 neurons (lines in top panel and single spikes in bottom panel), periods of 10 ms to several seconds of asynchronous high-rate activity, covering 10 to 40 neurons (wider bands in top panel and constant low-activity periods in bottom plot), and periods of silence between 10 and 800 ms. Inside the high-activity bands neurons spike with different frequencies, shown by the apparent horizontal stripes. Due to their differently sized feedback zones, neurons have different refractory periods. High rate activity bands in the network are triggered by clusters of 20-80 neurons responding at the same time. When these enter their refractory periods, other neurons respond, causing a period of self-sustained activity with neurons responding at their maximum frequency, which is different for different neurons. After 10 ms to several seconds the high activity dies out. However, after coincidences have triggered groups of 50 to

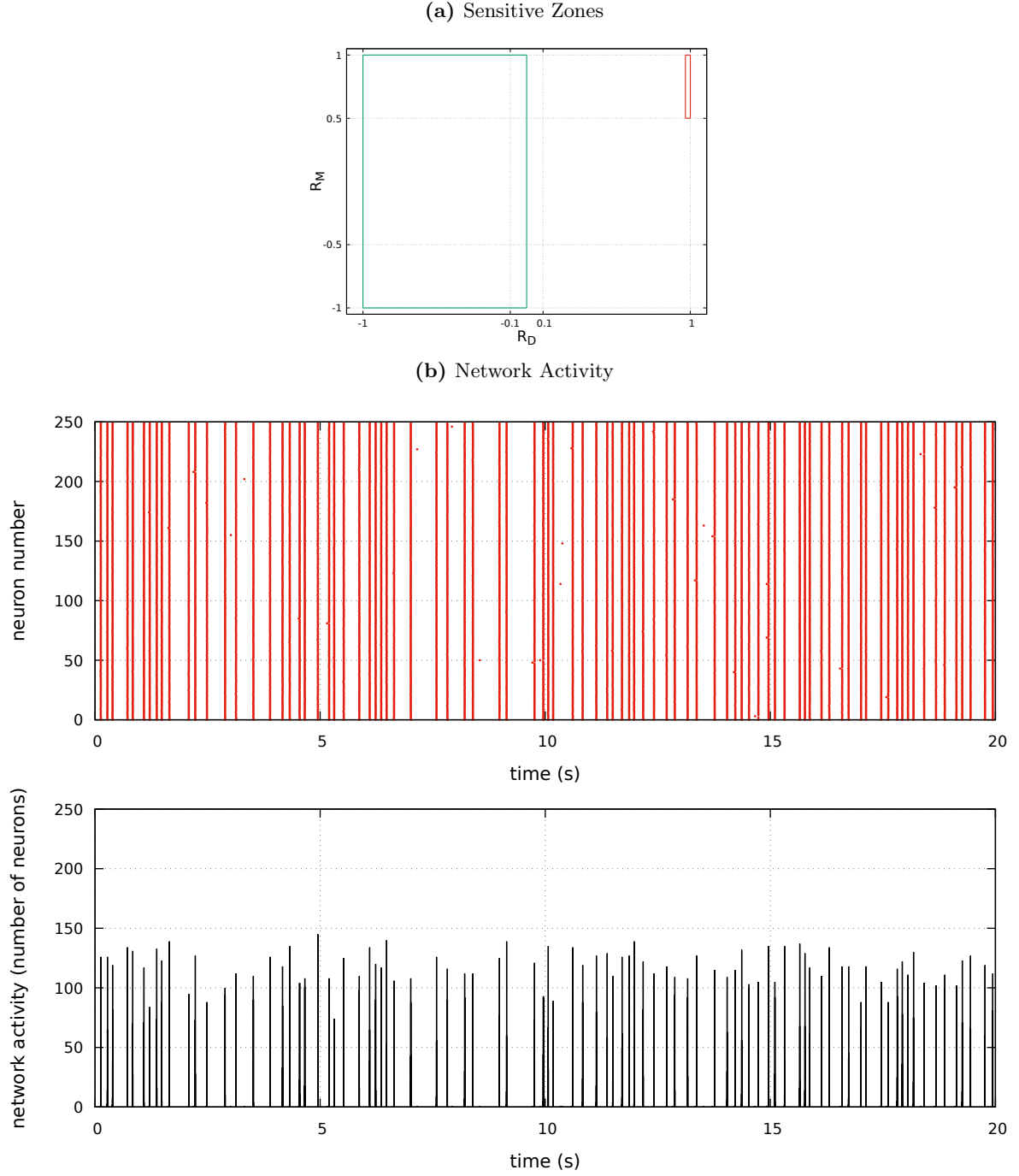


Fig. 10: Results for a network of coincidence detectors.

Sensitive Zones and activity of a network of 250 sparsely connected Difference Neurons, configured as coincidence detectors. (a): Sensitive Zones of Difference Neurons used in the network. The feedback zone (green) receives the neuron's response, the stimulus zone (red) receives the superimposed spike trains of the external stimulus and the pre-synaptic neurons. (b): Scatter plot of response firing (top) and total network activity (bottom). The scatter plot shows a point for each spike, neuron and time step. Note that for better visibility points for single spikes are larger than the distance between two neurons in the plot. The plot shows irregular synchronised responses that cover between 60 and 140 neurons. For explanation see section 4.6. For parameters see Table C4.

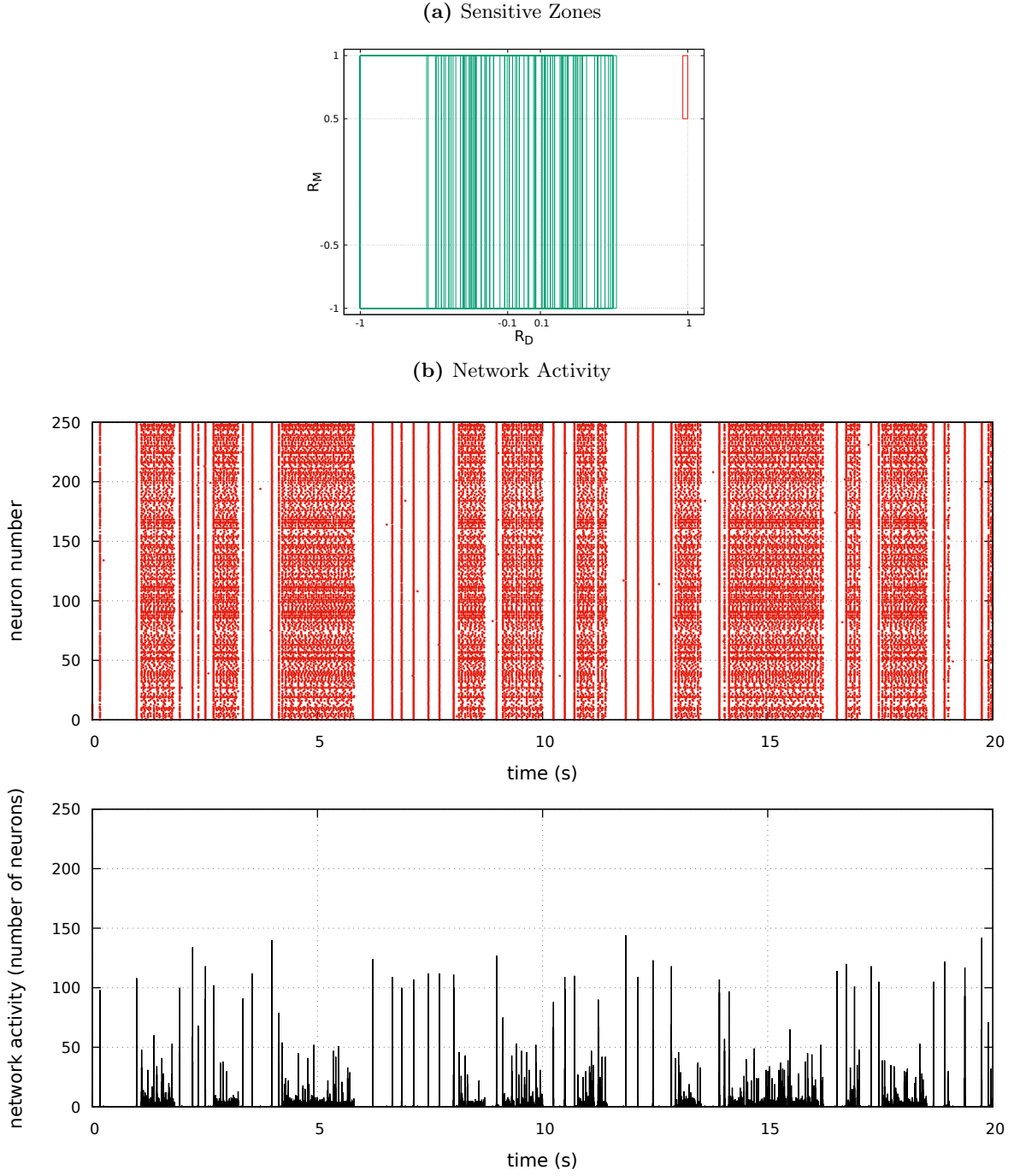


Fig. 11: Results for a network of coincidence detectors with distributed refractory periods.

Sensitive Zones and activity of a network of 250 sparsely connected Difference Neurons, configured as coincidence detectors. The minimum response frequency is different for every neuron. **(a)**: Sensitive Zones of Difference Neurons used in the network. The feedback zone (green) receives the neuron's responses. The maximum Neural Drive of the feedback zone is chosen randomly between -0.5 and +0.5. The stimulus zone (red) receives the superimposed spike trains of the external stimulus and the pre-synaptic neurons. **(b)**: Scatter plot of response firing (top), and plot of total network activity (bottom). For explanation see section 4.6. For parameters see Table C4.

150 neurons to respond at the same time, many more neurons enter their refractory period. Not enough neurons are left that could start a period of high activity and the synchrony remains one single event. This means, if response times are randomly distributed, a sparsely connected network of Difference Neurons configured as coincidence detectors can exhibit sharp synchronised irregular responses and longer periods of high activity, separated by intervals of silence. This is comparable to the network behaviour shown in other studies using different neuron models, and investigating *in vivo* and *in vitro* recordings (Tartaglia and Brunel 2017; Beiran et al. 2018; Perez-Zabalza et al. 2020).

How do temporal delays affect the network? Figure 12 shows a network consisting of neurons that respond to coincidences at a delay – the Sensitive Zone in Figure 12a is shifted to the left, $d^+ = 0.1$, and the neuron spikes 86 ms after a coincidence. The resulting network activity is seen in Figure 12b. The plot also shows synchronised events, but these events are slightly smeared out in time, and periods of no activity no longer exist (cf. Figure 10b). There is a constant synchronous low-activity background oscillation at a frequency of 11 Hz, shown in the bottom plot and in the power spectral density in an inset in Figure 12b. Due to the lower Neural Drive of the Sensitive Zones, several neurons spiking at the same time will not trigger a cascade of response spikes at the next instant, but only after a delay (here 86 ms), where the width of the Sensitive Zone allows for some variation in the response time. This causes coincident responses that would otherwise occur at the same instant to be spread out in time, effectively blurring spike volleys. For the same reason there is no longer a period of inactivity after a synchronised spike burst. Since a spike burst needs to be coincident to cause a response, and since a response will happen a fixed time (86 ms) later, all network activity appears as if modulated by fast oscillations. This means, a fixed delay can cause fixed-rate synchronous low-level activity. In a network of coincidence detectors, the

same delay can smooth out synchronous events in time, modulated by the fixed-rate oscillations.

Is it possible to set up a network that operates purely under inhibition? If yes, how does such an inhibitory network behave? Figure 13 shows a network of neurons that receive inhibitory stimuli only. The spike trains of the external stimulus and the pre-synaptic neurons in the network are superimposed and serve as input into the Difference Detector whose Sensitive Zone is located in the inhibitory region of the $R_{M,D}$ plane. Network activity starts with single neurons randomly and asynchronously showing spike bursts of one to ten single spikes. At a certain time the network state changes into fixed synchronised events with inter-event intervals of 210 ms, each event covering about half of the network’s neurons. If a neuron inhibits several post-synaptic neurons, these neurons will not spike while the neuron is active. After a certain time has passed since the stimulus was seen by their Difference Detectors, these post-synaptic neurons will spike, in turn inhibiting further neurons that they project to. Since the Sensitive Zones have the same size and position, the time after a spike is identical for all neurons. An avalanche of synchrony will sweep over the network, and once these oscillations have taken over, the network cannot go back into a different state again, since in the intervals between two responses all spiking is inhibited. This is why the non-synchronised state is transient. This means, running a network solely on inhibition is not possible using biological neuron models, but here the Difference Neuron allows to study the role of inhibition in isolation. The fact that inhibition can lead to synchrony is known, and a network of Difference Neurons can reproduce this.

Measuring the Neural Mode and Drive of biological spike trains has shown that most values lie on the diagonal between slow inhibition and coincidence detection (Kanev et al. 2016). How does the response behaviour of a neural network change, depending on the position of the Sensitive Zone along this diagonal? Figure 14 shows the results of seven numerical simulations, each with a duration of ten seconds and with the neuron’s

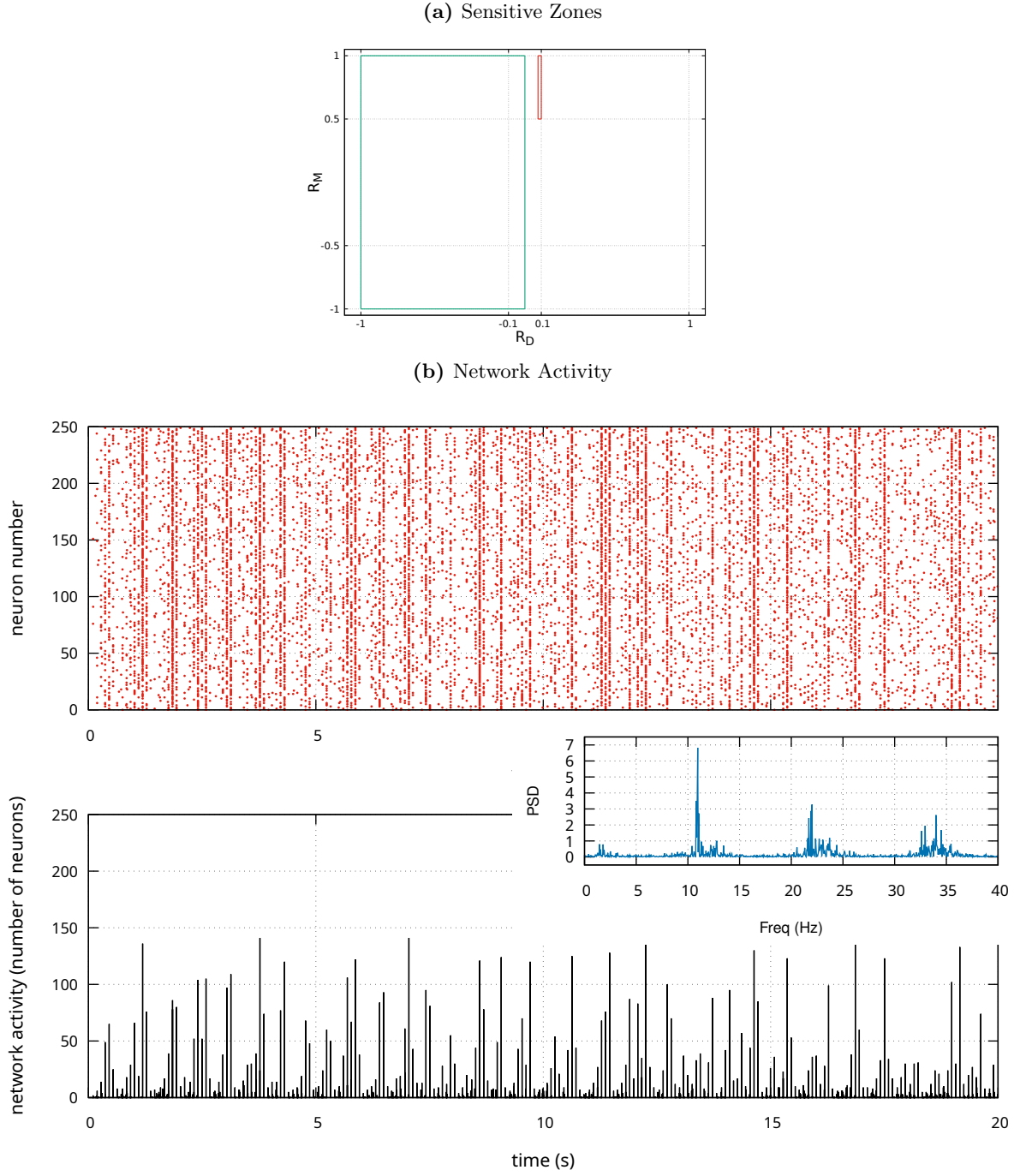


Fig. 12: Results for a network of coincidence detectors with delay.

Sensitive Zones and activity of a network of 250 sparsely connected Difference Neurons, configured as coincidence detectors with large delay. **(a)**: Sensitive Zones of Difference Neuron used in the network. The feedback zone (green) receives the neuron's response, the stimulus zone (red) receives the superimposed spike trains of the external stimulus and the pre-synaptic neurons. **(b)**: Raster plot of response firing (top), total network activity (bottom), power spectral density of total network activity (inset). All activity seems modulated by a constant rate of roughly 11 Hz. For explanations see section 4.6. For parameters see Table C4.

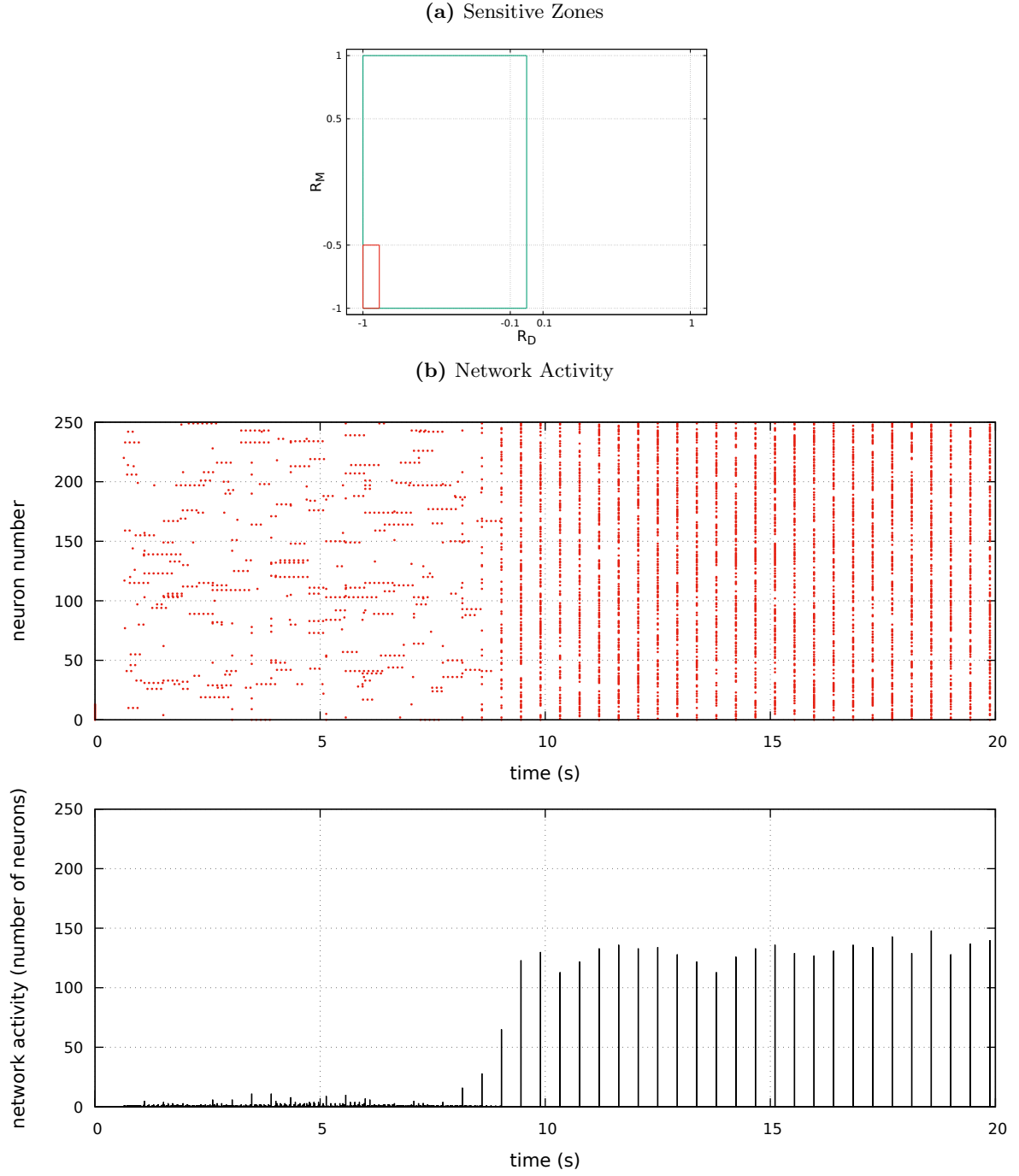
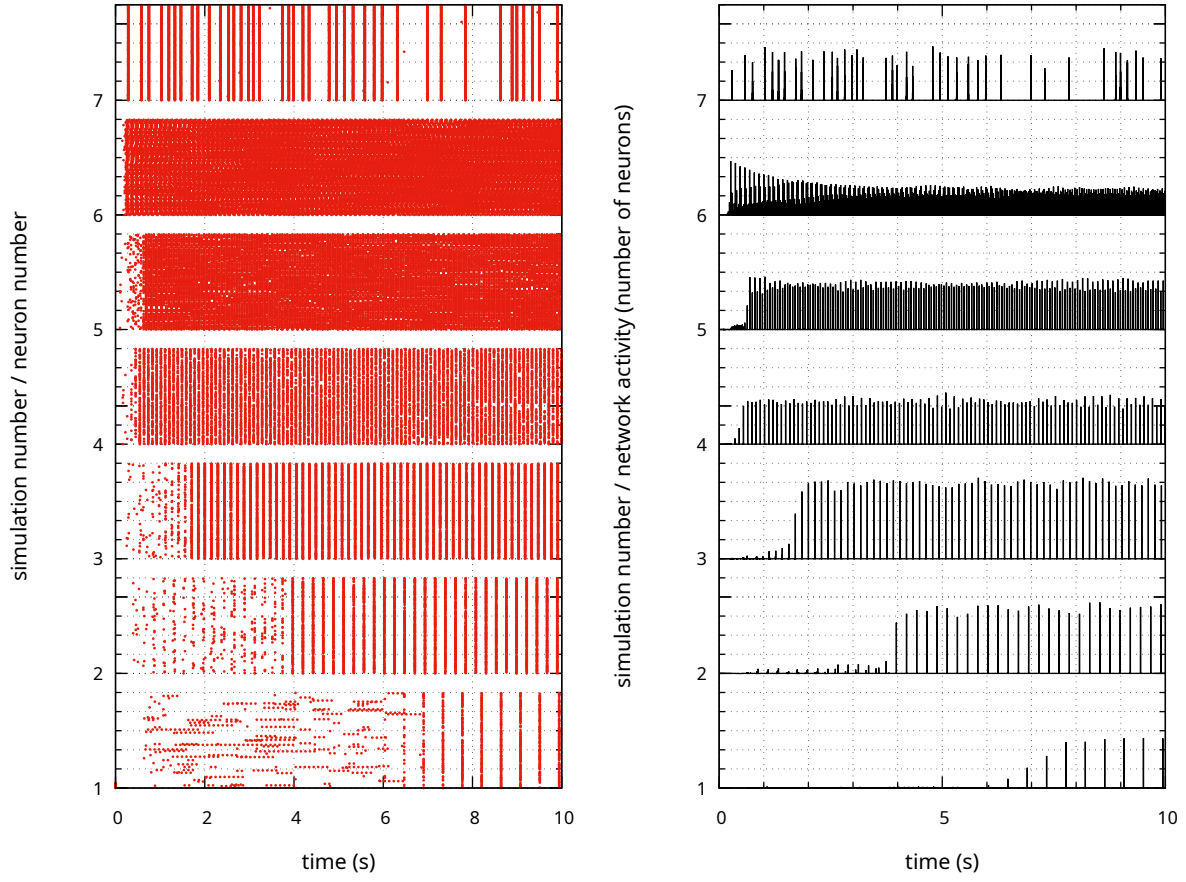


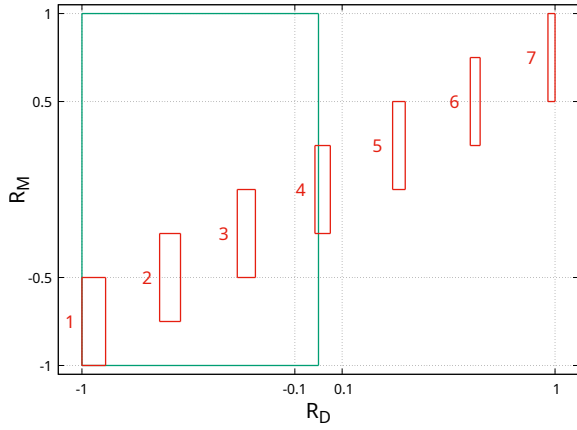
Fig. 13: Results for a network of Difference Neurons with inhibitory Sensitive Zones only.

Sensitive Zones and activity of a network of 250 sparsely connected Difference Neurons, configured using inhibitory Sensitive Zones. **(a)**: Sensitive Zones of Difference Neuron used in the network. The feedback zone (green) receives the neuron's response, the stimulus zone (red) receives the super-imposed spike trains of the external stimulus and the pre-synaptic neurons. **(b)**: Scatter plot of response firing (top) and total network activity (bottom). After a transient period of asynchronous activity the network changes into a state of synchronous oscillation of 4.76 Hz. For explanation see section 4.6. For parameters see Table C4.

(a) Network Activity



(b) Sensitive Zones



(c) Mean and Synchronisation

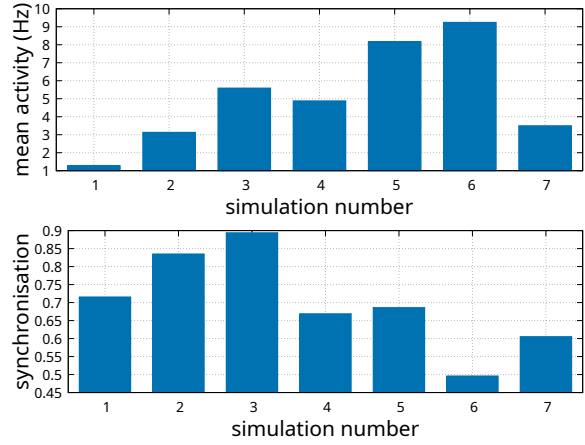


Fig. 14: Moving from slow inhibition to coincidence detection.

Sensitive Zones and activity of ten seconds simulated time in seven networks of 250 Difference Neurons each. (a) Left, red: Raster plot of network activity. Right, black: Total network activity. (b) Sensitive Zones for each simulation, starting with the lower left for the first simulation to the upper right for the last simulation. (c) Top: Activity mean of the last two seconds of each simulation, bottom: network synchronisation of the last two seconds of each simulation. For explanation see section 4.6. For parameters see Table C4.

Sensitive Zones in a slightly different shape and located at a different position. In the first simulation the Sensitive Zones are identical to Figure 13, in the last simulation they are identical to Figure 10, in between shape and position were interpolated between the first and the last parameter set. A raster plot and the summed network activity are shown in Figure 14a, the progression of the Sensitive Zone connected to the stimulus is shown in Figure 14b, the activity mean of the last two seconds in Figure 14c (top), and the network synchronisation according to equation B3 of the last two seconds (figure 14c, bottom). The first simulation shows an inhibitory network, starting with asynchronous activity. The second simulation shows a network with inhibition represented by slightly shorter delay times. For the next simulations, while moving the Sensitive Zone towards coincidence detection, the change to regular synchrony happens earlier, the synchronous frequency is higher, the network synchronisation increases and the total response mean increases. The last simulation shows an abrupt change to the previous synchronisation; the network displays the same synchronised behaviour as the delay-less coincidence detector network, the mean drops by half (see Figure 14c, top) and synchronisation increases slightly (see Figure 14c, bottom). The network moves from slow oscillation to fast oscillations and finally to an irregular synchronised state. The frequency of the synchronous activity is determined by the neurons' response delay, which is caused by the maximum neural drive border of the (Stimulus) Sensitive Zone. Moving the zone to the right decreases this delay and hence increases the frequency of the synchronous activity. The decreasing delay causes the change from asynchronous behaviour to synchronous behaviour to happen earlier – an increased number of synchronous responses in the same time effectively changes the time-scale of the neural response. Both Difference Detectors have the same multiplicity and normalisation, so their rectangular representations in the $R_{M,D}$ graphs are directly comparable. In the inhibitory regime the neurons' delay is defined by the stimulus zone. When the

stimulus Sensitive Zone is moved outside the borders of the feedback Sensitive Zone (i.e., when the red zone moves outside the green in Figure 14b), the minimum response delay is not determined by the right border of the stimulus zone, but by the right border of the the feedback zone. The oscillation caused by the stimulus zone is now so fast that this refractory period forces neurons to either skip a wave, or spike between two waves, depending on their pre-synaptic connections. In the last simulation without delay, the immediate response to a coincidence and subsequent refractory period causes the pattern of alternating asynchronous high-rate activity and random synchronisation events seen earlier. This is because the immediate response to a stimulus triggers all post-synaptic neurons at the same time, causing the refractory period to end an avalanche of spike synchronously for all neurons. This means, there is a direct relation between the Neural Drive and the oscillation frequency – a maximum Neural Drive smaller than one causes synchronisation with a frequency that is proportional to the Drive value. In general, the position and shape of the Sensitive Zones influences network oscillations, and defines regular as well as irregular synchronisation patterns.

4.7 Difference Neuron vs. LIF Neuron Models

Random walk neuron models with a nonlinear decay show a behaviour that resembles coincidence detection. Stimulus spikes that occur at a higher rate drive the membrane potential up faster than stimuli with a low spike rate. Thus, stimulus spikes with an inter-spike interval that is below a certain value can cause a response, while stimulus spikes that occur with longer intervals do not (Abeles 1982). This is precisely how the Difference Neuron works, although the Difference Neuron replaces this non-linear dependency between spike group width and response probability with a fixed rectangular Sensitive Zone. In this section we show in how far properties of random walk models – using a conductance-based leaky Integrate-and-Fire Neuron (LIF) as

an example – can be captured by a Difference Neuron. We simulated an LIF Neuron with three different parameter settings and fitted a Difference Neuron to each (details of parameters and fitting method in 3 and Appendix A).

How well does a simple Difference Neuron represent an LIF Neuron with one single conductance in a low response rate scenario? Figures 15a, 15b show a Difference Neuron fitted to an LIF Neuron responding with low rate (10 Hz). To achieve a low response rate without inhibition we used an unnaturally high threshold of 1 mV, resulting in a high effective mean membrane potential compared to the reset value V_0 of -70 mV and large resets after responses. The final error after fitting was 12 %, using a combined rate and variance cost function (see eqn. A1) that ranged from 0 (perfect match) to 1 (independence). Matching and timing of spike times are good, and apart from a few exceptions, spike timing is identical. The Sensitive Zones after fitting clearly show a coincidence detector. The membrane potential of the LIF Neuron (Figure 15b bottom) shows the neuron in a sub-threshold regime - the effective mean membrane potential during stimulation is below the threshold, and the neuron detects small fluctuations in the input. Small fluctuations trigger a response. Because of the non-linear membrane potential decay, positive fluctuations of the membrane potential are caused by stimulus spikes intervals that are narrower than usual. This is the idea the Difference Neuron is built upon, therefore a good agreement between Difference Neuron and Integrate-and-Fire Neuron is to be expected. This means, in a single-stimulus low-response-rate scenario a conductance based LIF Neuron acts like a coincidence detector. In this case the Difference Neuron behaves exactly like an LIF Neuron.

How does a simple Difference Neuron compare to an LIF Neuron with one single conductance in a high-response-rate scenario? Figures 15c and 15d show a Difference Neuron fitted to an LIF Neuron responding at a response rate of 100 Hz (achieved by a lower spiking threshold in order to keep all other parameters the same). The final error after

fitting was 27 %. The timing accuracy of the Difference Neuron compared to the LIF Neuron was not as good – the Difference Neuron reflects the local mean rate quite well, but single spikes do not match any more. The Sensitive Zones after fitting show the Difference Neuron to operate more like an integrator since the excitatory Sensitive Zone is not confined to the coincidence detection range of $R_M > 0.5$ but extends well down into the area of integration. The LIF neuron (figure 15d bottom) operates in a super-threshold regime – the theoretical effective mean membrane potential in absence of the threshold, during stimulation is above the actually existing threshold. Apart from using theoretical calculations, or plotting without spiking threshold, it is the firing of a response after almost exactly five stimulus spikes, that shows this. Stimulus inter-spike interval sizes are mostly ignored, and the LIF Neuron has effectively turned into a spike counter. Using a design idea that is based on measuring inter-spike distances and that captures the working of a coincidence detector, it is not possible to implement a spike counter – at least not with one single stimulus zone. To achieve this, multiple stimulus and response zones at different multiplicities would be necessary. This means, in a single-stimulus high-response-rate scenario, a conductance based LIF Neuron is a temporal integrator. In this case the Difference Neuron captures overall frequency fluctuations, but not single response times any more.

How well would a Difference Neuron reflect the response of an LIF Neuron driven by balanced excitation and inhibition? Figure 16 shows a Difference Neuron fitted to an LIF Neuron responding with a low rate (10 Hz) to input from one excitatory and inhibitory conductance at 500 Hz respectively. The final error after fitting was 16 %, not as good as in the single-stimulus setting, but more accurate than in the high-rate scenario. The Sensitive Zones show coincidence detection with respect to the excitatory and inhibition with respect to the inhibitory stimulus. The effective membrane potential of the LIF Neuron (Figure 16b) is much lower and shows much higher variance than in the single stimulus setup (Figures

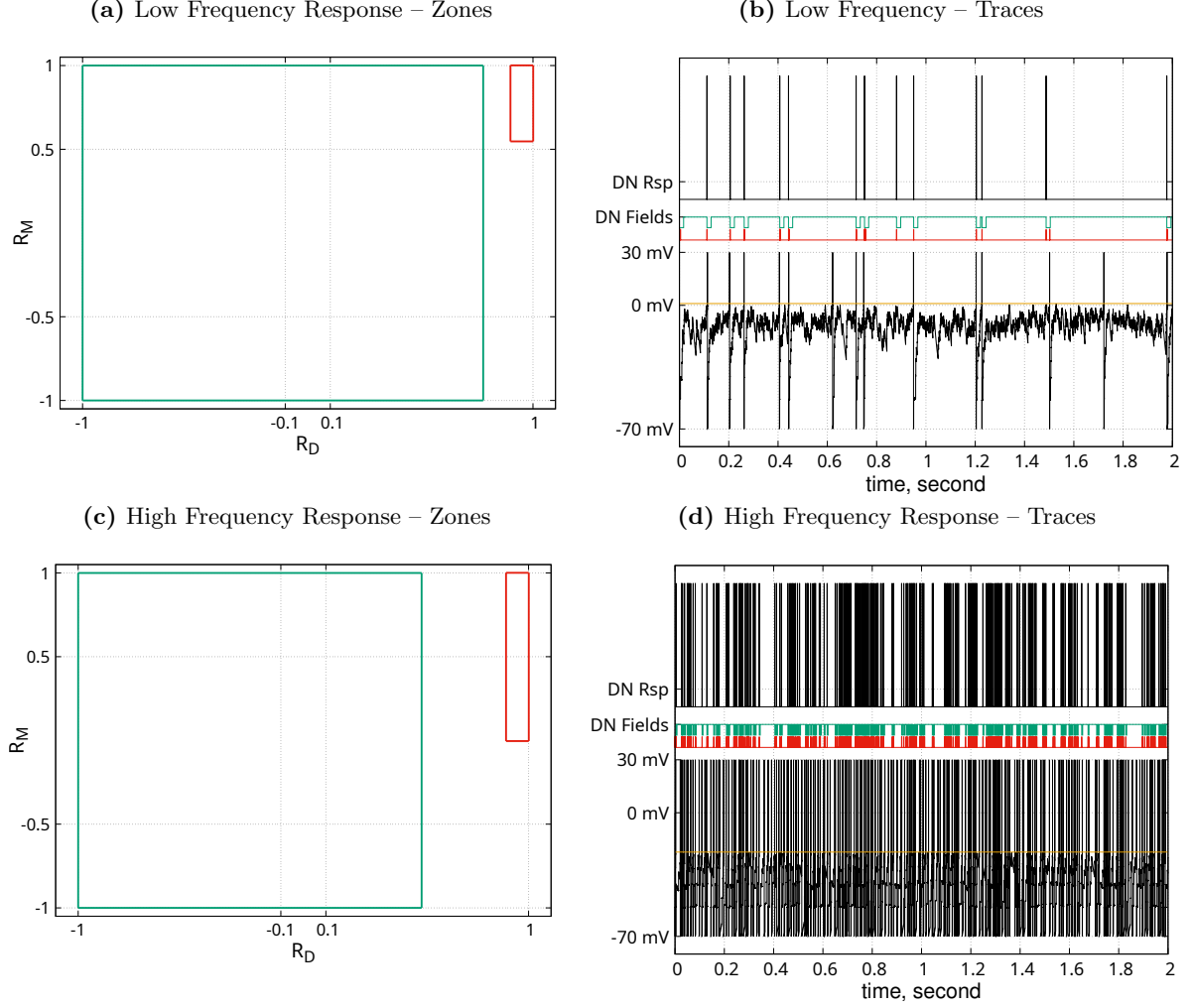


Fig. 15: Two Difference Neurons fitted to two LIF Neurons with excitatory conductance.

(a): Sensitive Zones of a Difference Neuron after fitting to an LIF Neuron with one excitatory conductance, a stimulus rate of 500 Hz, and a response rate of 10 Hz. Red – excitatory Sensitive Zone, green – feedback Sensitive Zone. (b): Samples of the Difference Neuron’s response (top, black), the activity of its Difference Detectors (middle; red – excitatory, green – feedback), and the LIF Neuron membrane potential (bottom, black) for the same neuron, the orange line denotes the spiking threshold. (c): Sensitive Zones of a Difference Neuron after fitting to an LIF Neuron with a stimulus rate of 500 Hz, one excitatory conductance, and a response rate of 100 Hz. (d): Samples of the Difference Neuron’s response (top), the activity of its Difference Detectors (middle), and the LIF Neuron membrane potential and spiking threshold (bottom) for the same neuron. Colours as above. For explanation see section 4.7. For parameters see Table C5.

15b and 15d), and the LIF Neuron operates in a sub-threshold regime. The inhibitory stimulus suppresses answers. If the single-time Neural Mode and Drive, $R_{M,D;t}$, of an LIF were measured, the result would show two non-rectangular point clouds in the $R_{M,D}$ plane, for inhibitory and excitatory Mode and Drive respectively. The Difference Neuron estimates these by rectangular Sensitive Zones, discarding any temporal relations

that go beyond inter-spike group sizes. However, since the LIF Neuron is a coincidence detector (see the original work on the Neural Mode and Drive (Kanev et al. 2016) for exact measurements), the Difference Neuron reflects its behaviour well. This means, although the Difference Neuron in the two-stimuli setup does not approximate an LIF Neuron as well as in the single-stimulus setup,

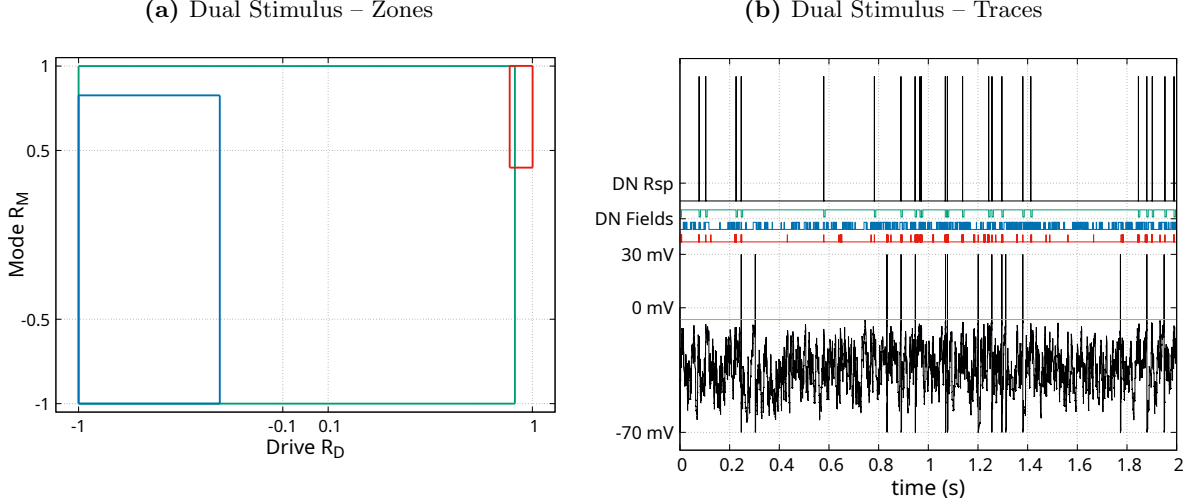


Fig. 16: Difference Neuron fitted to an LIF Neuron with excitatory and inhibitory conductances.

(a): Sensitive Zones of a Difference Neuron after fitting to an LIF Neuron with two conductances, an excitatory stimulus rate of 500 Hz, an inhibitory stimulus rate of 500 Hz, and a response rate of 10 Hz. Red – excitatory Sensitive Zone, blue – inhibitory Sensitive Zone, green – feedback Sensitive Zone. (b): Samples of the Difference Neuron’s response (top, black), the activity of its Difference Detectors (middle; red – excitatory, blue – inhibitory, green – feedback), and the LIF Neuron’s membrane potential (bottom, black). The spike threshold is denoted by the orange line. For explanation see section 4.7. For parameters see Table C5.

a Difference Neuron can approximate the dependence of an LIF Neuron’s response on both its excitatory and inhibitory stimuli.

How does a Difference Neuron compare to an LIF Neuron over a range of stimulus rates? How does a simple single-zone Difference Neuron respond during a regime change, where a stimulus of increasing rate would take an LIF Neuron from a sub-threshold coincidence-detection regime to a super-threshold temporal-integration regime? Figure 17 compares response mean, CV, and Neural Mode of two Difference Neurons (static and dynamic) and one conductance-based LIF Neuron, while the stimulus rate drove the LIF Neuron response from a low to a high rate. The LIF and Difference Neurons from the previous simulations were used – fitted to respond at 10 Hz spike rate to a stimulus spike train of 500 Hz. Figure 17c shows the Difference Neurons’ Sensitive Zones. Figure 17a shows mean (top) and CV (bottom) of all three model neurons plotted against the stimulus rate. Each point in the curve was computed by using a numerical simulation over 500 simulated seconds. Figure 17b shows the Neural Mode and Neural Drive of all three neurons. The Mode

and Drive were calculated using expected stimulus intervals based on the respective current stimulus rate ($1/r_0^* = 1/r_N^* = \text{stimulus rate}$). Figure 18 compares sample spike trains and ISI distributions at stimulus rates of 500 Hz (Figures 18a and 18d), 900 Hz (Figures 18b and 18e) and 1300 Hz stimulus rate (Figures 18c and 18f). These values are also marked in the plots of Figure 17 by blue vertical lines. At a rate of 500 Hz, the Difference Neuron’s ISI distribution is a near-perfect match of the LIF’s (Figures 18a and 18d). The static Difference Neuron’s response generally shows the same non-linear increase in rate and decrease in CV as the LIF’s response, but both stay below the LIF’s mean and CV. The static Difference Neuron saturates at an earlier stage than the LIF (Figures 17a top, and 18c). $R_{M,D}$ values for LIF Neuron and static Difference Neuron show that both neurons are coincidence detectors at low response rates, changing to temporal integrators at high response rates. This effect is much more pronounced in the Difference Neuron than in the LIF. In addition, the static Difference Neuron increases its response delay (purple curve in Figure 17b). The dynamic Difference Neuron

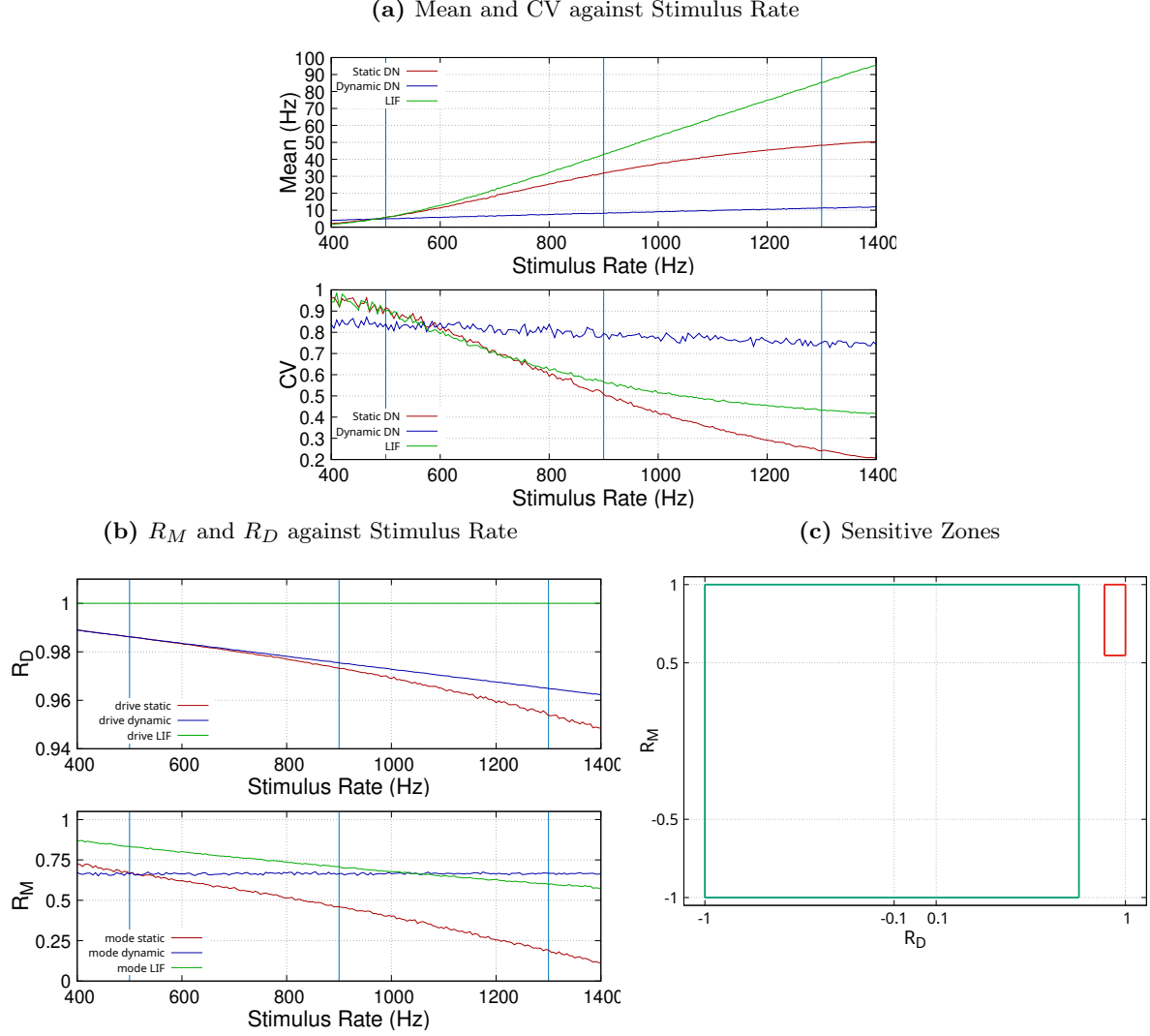


Fig. 17: Changing the stimulus rate for an LIF, a static, and a dynamic Difference Neuron.

Activity and Sensitive Zones of a static Difference Neuron, a dynamic Difference Neuron, and an LIF Neuron, during an increase in stimulus rate from 400 Hz to 1400 Hz. Difference Neuron parameters were fitted for a stimulus rate of 500 Hz. Snapshots of spike trains obtained at stimulus rate values of 500 Hz, 900 Hz, and 1300 Hz, marked by vertical blue lines in (b) and (a), are shown in Figure 18. (a) Mean (top plot) and CV (bottom plot) of all three model neurons, plotted against stimulus rate. The mean and CV of the LIF, dynamic, and static Difference Neuron are plotted in blue, red, and green. (b) Neural Mode and Neural Drive of all three neurons, plotted against stimulus rate. (c) Sensitive Zones of the static and dynamic Difference Neurons. R_M , R_D , mean, and CV curves of the static Difference Neuron are plotted in red, curves of the dynamic Difference Neuron are plotted in blue, curves of the LIF in green. For explanation see section 4.7. For parameters see Table C6.

shows a slight increase in rate and decrease in CV, both almost linear, and has a fixed Neural Mode throughout the whole stimulation frequency range.

Saturation happens when the Difference Neuron sees a high-rate stimulus as a high-density train full of spike coincidences. The Sensitive

Zone is active almost all of the time, and the refractory period starts to determine the response interspike-interval size. In Figures 18e and 18f, the static Difference Neuron (red) and the LIF Neuron (green) show an increasingly narrow distribution (compare the different resolutions of the x-axis, and the increasing height of the peak), while

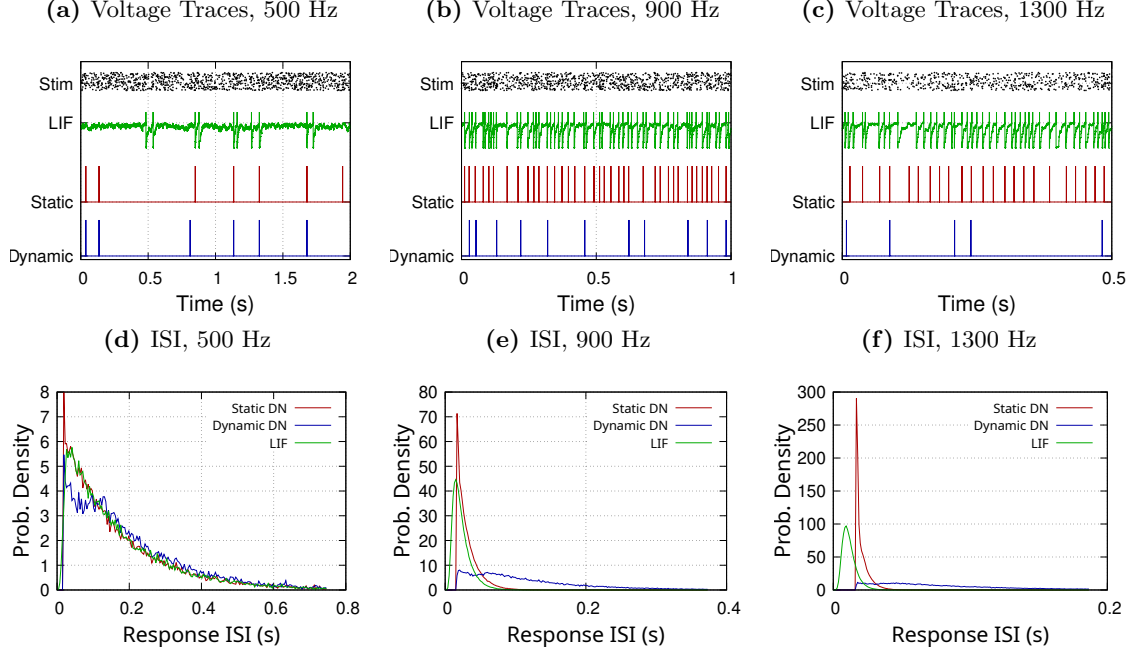


Fig. 18: Spike train and ISI distributions for an LIF, a static, and a dynamic Difference Neuron.

Single simulations from the parameter exploration shown in Figure 17. **(a)** Stimulus (top, black), membrane potential of the LIF Neuron (green), response of the static Difference Neuron (red), and response of the dynamic Difference Neuron (blue) at a stimulus rate of 500 Hz. The single Stimulus events are plotted in a band for better visibility. **(d)** Interspike-interval distribution of the dynamic Difference Neuron (blue), the static Difference Neuron (red) and the LIF Neuron (green) at 500 Hz. **(b)** Stimulus (black), membrane potential of the LIF (green), response of the static (red) and of the dynamic Difference Neuron (blue) at 900 Hz. **(e)** Interspike-interval distribution of the dynamic Difference Neuron (blue), the static Difference Neuron (red) and the LIF Neuron (green) at 900 Hz. **(c)** Stimulus (black), membrane potential of the LIF (green), response of the static (red) and of the dynamic Difference Neuron (blue) at 1300 Hz. **(f)** Interspike-interval distribution of the dynamic Difference Neuron (blue), the static Difference Neuron (red) and the LIF Neuron (green) at 1300 Hz. For explanation see section 4.7. For parameters see Table C6.

the dynamic Difference Neuron’s ISI distribution (blue) changes much less. The spike train plots in Figures 18b and 18c of both the static Difference Neuron and the LIF Neuron show increasing regularity. An LIF Neuron by design cannot respond at a latency, each response happens without delay after a stimulus spike. The changing Neural Mode and Drive of the static Difference Neuron is caused by the way the $R_{M,D}$ is calculated in Figure 17b – the neuron’s responses are produced by a Sensitive Zone that compares all stimulus intervals to an interval size of 2 ms (equivalent to a 500 Hz stimulus), however, the $R_{M,D}$ values in Figure 17b are calculated by comparing all stimulus intervals to the current mean inter-stimulus interval in the stimulation and thus show the static Difference Neuron moving from coincidence detection to

temporal integration. A dynamic Difference Neuron here behaves differently than both the static Difference Neuron and the LIF, by remaining a firm coincidence detector throughout the whole stimulation range.

This means, increasing the stimulus rate drives an LIF Neuron from low-rate, coincidence detection, to high-rate, integration responses. A static Difference Neuron with a single stimulus Sensitive Zone reflects this change, although the exact values of mean, CV, and $R_{M,D}$ differ. ISI distributions match well for the coincidence detection regime. At higher response rates the ISI distributions of both a static Difference Neuron and an LIF Neuron get narrower. A dynamic Difference Neuron does not change its Neural Mode and Drive, by design.

4.8 Networks of Difference Neurons and Integrate-and-Fire Neurons

How does a Difference Neuron compare to an Integrate-and-Fire Neuron in a network setting? We created three identically connected networks (randomly connected with 10% connection probability) composed of static Difference Neurons, dynamic Difference Neurons, and LIF Neurons, respectively. We used the parameters of the previous simulations in the network – the LIF Neurons respond at 10 Hz to a stimulus of 500 Hz, and the Difference Neurons’ Sensitive Zones were fitted to reproduce the behaviour of the LIF, receiving the identical 500 Hz stimulus. Each neuron receives random Poisson distributed external input; equivalent neurons in the three networks receive identical input. Both simulations were preceded with 0.3 seconds of standard rate stimulus (460 Hz for the one-rate plot and 300 Hz for the two-rate plot, not shown in the plots) to initialise the dynamic neurons. Figure 19a shows the network activity during stimulation with a 460 Hz Poisson stimulus spike train to each neuron (stimulus shown in Figure 19c). Figure 19b shows activity during stimulation with two different frequencies (high rate stimulation of 600 Hz and low rate stimulation of 300 Hz, shown in Figure 19d). The LIF Neuron network (green dots and lines in Figures 19a, 19b) shows irregularly occurring flashes of synchronisation (vertical lines). The network of static neurons shows similar behaviour, with fewer synchronous events. The LIF Neuron network and the static Difference Neuron network both go into saturation (i.e., high rate oscillations at the maximum frequency the refractory time allows) during high rate inputs but remain in a low-activity non-synchronised state at low input rates. However, the dynamic Difference Neuron network, while going into saturation at the high-rate stimulus periods briefly, quickly adapts. After the high-rate stimulation the dynamic network goes into a very low response mode, but adapts quickly again. During the low rate stimulus the network shows random synchronised events, much like in Figure 19a. This means, the main network activity follows the same trend in a Difference Neuron and

a LIF Neuron network. While the activity and synchronisation of the LIF Neuron network and a network of static Difference Neurons is heavily dependent on the stimulus rate, the adaptive Difference Neurons maintain a similar firing pattern at different stimulus intensities.

How do the total activity and the network synchronisation change when the stimulus rate changes? We varied the stimulus rate between 350 Hz and 500 Hz and measured the total activity and the network synchronisation according to equation (B3). Figure 20 shows the results; each data point is the average of 18 simulations for each the three randomly connected networks with 100 neurons, and stimulated for 10.0 seconds. For the LIF Neuron network (green curve in Figures 20a and 20b), the mean activity seem to rise exponentially below a frequency of 400 Hz and change its exponents for higher stimulus frequencies, while the synchrony stays at a fixed level of 0.1 below a stimulus rate of 400 Hz and then grows fast to almost 0.4. The static Difference Neuron network (red curves) shows an exponentially growing response rate and a non-linearly growing synchrony, but at lower values than the LIF. The network of dynamic Difference Neurons keeps an almost constant network activity level and synchronisation level independent of input frequency. Figure 17a shows that the rate change of single LIF, static, and dynamic Difference Neurons in response to increasing stimulus is linear or sublinear. The exponentially growing response rates of the LIF Neuron and of the static Difference Neuron networks are therefore caused by recurrent intra-network input. The increase in noise (right part of the green curve in Figure 20a) is caused by the fact that differently connected networks have vastly different response properties, this difference increases with higher rate stimulus for the chosen parameters, and was not fully smoothed out by the averaging. The higher sensitivity of the LIF Neuron to stimulus rate changes (Figure 17a), compared to the static and the dynamic Difference Neuron, explains the larger rate of the LIF Neuron network compared with the exponential rate growth of the static Difference Neuron

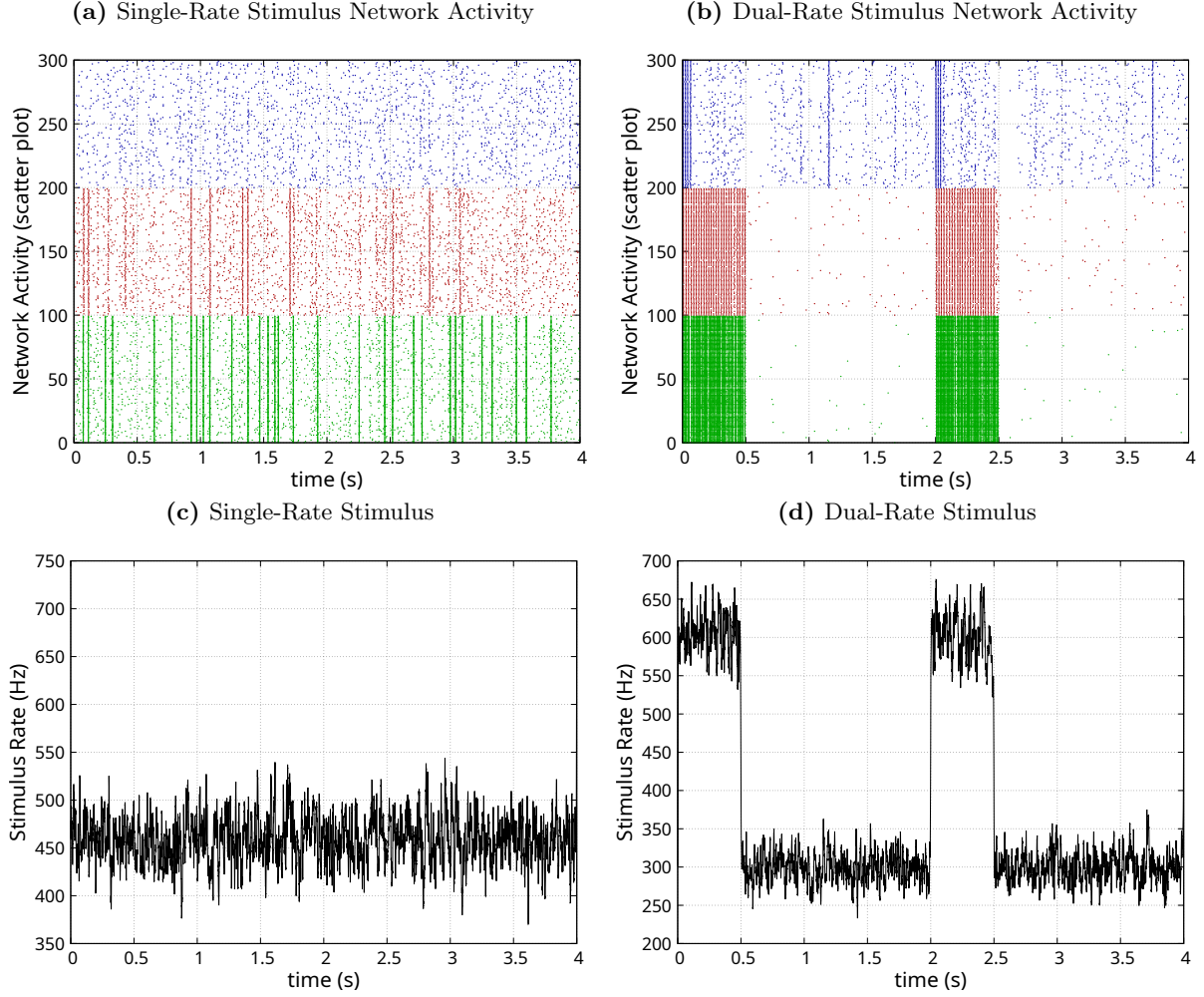


Fig. 19: Networks of LIF Neurons, static Difference Neurons, and dynamic Difference Neurons.

Stimulus and response activity of a sparsely connected network of 100 dynamic Difference Neurons (blue), an identically connected network of 100 static Difference Neurons (red), and an identically connected network of 100 LIF Neurons, using Difference Neurons that were fitted to LIF neurons at a stimulus rate of 500 Hz. All three networks received identical stimuli. **(a)** Network activity while each neuron was being stimulated with an independent Poisson stimulus spike train of 460 Hz for 4 s. Neurons 0-99 (green): LIF Neuron network. Neurons 100-199 (red): static Difference Neurons. Neurons 200-299 (blue): dynamic Difference Neurons. **(b)** Network activity while neurons were stimulated with alternating rates of 600 Hz and 300 Hz. **(c)** Total input spike rate (considering input spikes to all neurons in one network, normalised per neuron) corresponding to **(a)**. Data slightly smoothed. **(d)** Total input stimulus spike corresponding to **(b)**. Data slightly smoothed. For explanation see section 4.8. For parameters see Table C7.

network and the slowly growing response rate of the dynamic Difference Neuron network. Since the stimuli to the single neurons were independent, all synchrony in the networks is caused by intra-network connections. This means, a network of static Difference Neurons can reflect the dynamics of synchrony and mean activity of a network of LIF Neurons, although, in this example both output rates and synchrony are higher for the LIF

Neuron network. A network of dynamic Difference Neurons keeps its operational mode such that its activity and synchronisation stay similar over a wider range of stimulus rates.

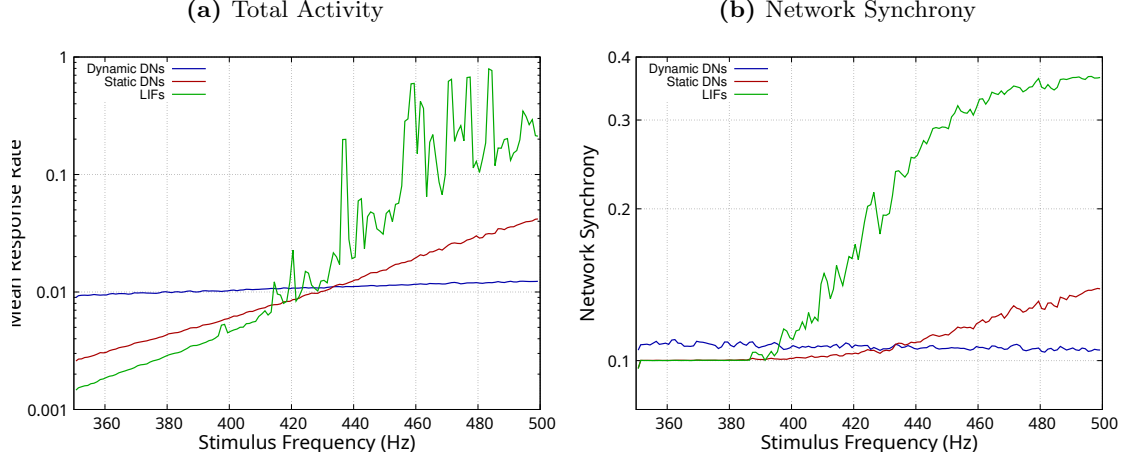


Fig. 20: Network activity and synchrony.

Average of response rate, and of network synchrony, plotted against stimulus frequency. **(a)**: Total network activity of the static Difference Neuron network (“Static DNs”, cyan), the dynamic Difference Neuron network (“Dynamic DNs”, purple), and the LIF Neuron network (“LIF”, blue). The y-axis has a logarithmic scale. **(b)** Network synchrony according to equation (B3) of static Difference Neuron network (“Static DNs”, red), dynamic Difference Neuron network (“Dynamic DNs”, blue), and LIF Neuron network (“LIFs”, green). The y-axis has a logarithmic scale. For explanation see section 4.8. For parameters see Table C7.

5 Discussion

The Difference Neuron has no hidden states. Its response is created directly from time distances of the latest pre-synaptic spikes. No reset interrupts its mathematical operation as in classical SDE-based random walk models where the SDE is only defined between two response spikes. All the model does is to constantly record how long ago the latest spikes occurred and check whether these values are within a fixed range. The neuron model is easy to implement, the only mathematical operations are comparisons and subtractions (and, in the case of the dynamic Difference Neuron, one multiplication for each stimulus spike), no differential equations need to be simulated.

The Neural Mode position of the stimulus zone determines whether the neuron responds after coincident stimulus groups, after spike groups forming large gaps, or is indifferent to the stimulus inter-spike interval (cf. Figure 1). The Neural Drive position of a Sensitive Zone determines the delay of the neural response with larger delays causing effects similar to inhibition (see (Kanev et al. 2016) on a discussion how different values of the Neural Drive represent different values of excitation or inhibition). A neuron can be configured

to operate at a certain Neural Drive at any point between the extremes of strong inhibition and strong excitation by simply placing a Sensitive Zone in the corresponding region of the Neural Drive continuum (cf. Figure 1). When moving the stimulus zone, the measured Neural Mode and Drive of the Difference Neuron change accordingly. The relation of response rate and response CV to the Neural Drive position of the stimulus zone is more complex, in particular when bursting is involved. In general, higher drive means higher response rate.

If the absolute width of the stimulus zone is larger than the gap between the right border of the feedback zone and 1.0, a Difference Neuron shows spike bursts. The maximal length of a burst depends on the width of the stimulus zone, the inner-burst frequency depends on the right border of the feedback zone. Using the multiplicity parameter N , Difference Neurons can be made sensitive to incoming bursts of a certain size N .

Combining excitation and inhibition creates a neuron that acts in a similar way to a natural neuron driven by balanced input. Coincidences in the excitatory stimulus can trigger a response, unless there is an inhibitory stimulus present at the same

time. Using two Sensitive Zones on top of each other a neuron can detect coincidences between separate stimulus spike trains. ISI detectors sensitive to more complex temporal relations can be created by placing multiple Sensitive Zones into different parts of the $R_{M,D}$ plane.

The dynamic Difference Neuron can keep its response rate within a limited range, even over a large range of stimulus frequencies. It also shows a high response CV when stimulated with a high input frequency; similar to the high irregularity at high firing rates that has been observed in cortical neurons in vivo (Softky and Koch 1993; Softky 1992), which cannot be reproduced by the LIF Neuron model (Bugmann et al. 1997). In addition, different ways of measuring the Neural Mode – using different normalisations or dividing the stimulus into different parts that are measured separately – correspond to multiple ways a static Difference Neuron can be defined; which could be either integrating or detecting coincidences, possibly using multiple separate Difference Detectors. This supports similar results that have been found in (Koutsou et al. 2012; Zavou et al. 2017).

A network of Difference Neurons configured as coincidence detectors can randomly switch between periods of asynchronous high-rate activity and sharp synchronised random responses. This is interesting because similar behaviour has been found in vivo (Luczak et al. 2007; Steriade M 1993; Metzen et al. 2020) and in attractor network models in other studies (Lundqvist et al. 2010; Protachevich et al. 2019). Delays, which we caused by the Sensitive Zone having a right border at $R_D < 1.0$, can turn synchronous network bursts into longer periods of high-rate activity. The position and shape of the Sensitive Zone influences network oscillations, and its parameters determine whether regular or irregular synchronisation patterns occur.

Since we based the Difference Neuron on the Neural Mode and Drive – a mathematically broad measure of neural operation – the neuron can exhibit response properties that other biological neuron models do not show. The Difference Neuron can spike in the absence of input signals, in

a regular fashion, similar to pacemaker neurons that operate solely on linear leak currents (Zhao et al. 2010). In contrast to neurons in a biological setting whose spikes would be a response to their excitatory stimulus, a Difference Neuron can respond to input that is solely inhibitory. The Difference Neuron can show gap detection (responses after a wide stimulus spike pair) or slow inhibition (only being blocked by inhibitory stimuli of low, but ignoring inhibitory stimuli of high frequency). Since the Difference Neuron can exhibit bursting (while an LIF Neuron cannot, unless it is equipped with a partial reset (Bugmann et al. 1997) or a variable threshold mechanism (Wilbur and Rinzel 1983; Kobayashi et al. 2009)), it is a comparable but more versatile model than the LIF Neuron. Networks of inhibitory biological neuron models remain silent, but here the Difference Neuron allows to study the role of inhibition in isolation. The fact that inhibition can lead to synchrony is known (Brunel and Hakim 1999), and a network of Difference Neurons can reproduce this. The mechanism by which the oscillations are generated is based on the notion that effects of inhibition can be described as a form of delay.

A Difference Neuron is a good approximation of a conductance based LIF Neuron. When the LIF Neuron operates in a sub-threshold coincidence-detection regime, the Difference Neuron can reproduce the spike response of the LIF Neuron from the same stimulus, although it does not provide a perfect match. In a temporal-integration super-threshold regime, the Difference Neuron captures overall frequency fluctuations, but no longer the single spike times. Increasing the stimulus rate drives an LIF Neuron from a low-rate response and coincidence detection to a high-rate response and integration. A single-zone static Difference Neuron reflects this change, although the exact values of mean, CV, and $R_{M,D}$ differ. ISI distributions match well for the coincidence-detection regime, but at a higher response rate the ISI distributions differ due to the limited refractory period of the Difference Neuron.

In a network of static Difference Neurons, after a stimulus rate change, response synchrony and

mean activity change in the same direction as in a network of LIF Neurons, but by a different amount. A network of dynamic Difference Neurons adjusts its operational mode such that the activity and synchronisation stays similar over a wider range of stimulus rates. Biologically this is interesting, because high CV on high response rates (as shown in a dynamic Difference Neuron, but unlike an LIF Neuron can show) has been observed in vivo (Softky and Koch 1993).

A perfect integrator, i.e., a neuron that responds with a rate proportional to its stimulus rate by counting stimulus spikes, cannot be constructed using a Difference Neuron. Spike counting would require an internal variable and the Difference Neuron is a memory-less machine by design. It is, however, possible to combine various stimulus and feedback Difference Detectors in a way that a Difference Neuron can approximate a perfect integrator by responding with fixed response rates to specific stimulus rate ranges, or it is possible to use a Sensitive Zone with dynamic r_0^* estimation for a similar effect.

6 Conclusion

Most of the current research into spiking neural networks utilises random walk models (Azghadi et al. 2021; Susin and Destexhe 2021; Yamazaki et al. 2022; Mobbille et al. 2024; Stoll et al. 2024; Huo et al. 2025). Difference Neurons make it much easier to analyse the role of integration or coincidence detection in a network. Since Sensitive Zones are defined by the range of their operational mode, neurons can combine coincidence detection, broad integration, or gap detection zones on the same stimulus, and their activity can be recorded at runtime during the operation of the network. The zone’s ranges can also be changed in a controlled way to examine the influence on the network’s behaviour.

Using Difference Neurons it is simple to hand-tailor neurons and networks that process their stimuli in specific manners. The neuron can create spike bursts, and the inner-burst frequency as well as the maximal burst length can be controlled by

the Sensitive Zone’s shape. Bursts can be an effective way to transmit information along a chain of Difference Neurons and Difference Detectors can be made sensitive to incoming bursts of a specific burst length or inner-burst frequency, or can be made to selective to stimuli from a pre-synaptic population of a certain size. Neurons with multiple zones could be used to model complex feature detection and signal processing chains. A setup with multiple excitatory zones could, for example, be used to model binaural sound localisation as proposed in (Jeffress 1948) or the behaviour of rate-phase coding in place cell networks of rodents (Monaco et al. 2019; Müller-Komorowska et al. 2023). Neurons with different zones that are sensitive to different frequencies can be cascaded to create networks that are sensitive to certain frequency patterns.

Importantly, connection strengths, inhibition or excitation, coincidence detection, or (pseudo) integration are defined as properties in time. The Difference Neuron does not implement inhibitory connections via signal values that are subtracted. Rather, the effects of inhibition and excitation are captured by time-delays between stimulus and response spikes. Dynamic rate estimation allows Difference Neurons to adapt their processing speed to the time scale of their stimulus. Difference Neurons, and connected networks of Difference Neurons, have no other parameters than time distances, and they operate on and produce sets of time points. This simplifies implementing certain time-related behaviour with Difference Neurons, e.g., delays between neurons can be defined by the zone position, and memory can be created by chaining neurons with delays.

Next steps would be to use the model for practical purposes, either to investigate the role of excitation or inhibition on network dynamics, to build simple real-world examples of networks for a given task, to explore non-biological modes like gap detection and fast inhibition, or to find easier explanations for more complex dynamics of single biological neurons. Because of its simplicity, the Difference Neuron lends itself to neuromorphic computing. Using Difference Neurons, many

more neurons could be packed into a single chip than using models that mimic ion channel based activity of biological neurons, while still using the approach of spike-based information processing.

All explanations and examples in this work describe neurons with fixed Sensitive Zones. Biological neural networks, however, are able to adapt their response behaviour. Learning algorithms as have been discussed earlier at conferences and workshops (see abstracts (Kanev et al. 2018, 2022)) may allow a single Difference Neuron to adjust the position of its Sensitive Zones by receiving training signals from a trainer neuron, re-creating the trainer neuron’s response to a stimulus. Layered networks can be constructed, using different forms of back-propagation. If those algorithms lead to stable learning, networks of Difference Neurons could be trained as universal machines for pattern recognition or for pattern generation, and the way biological neural networks learn could be understood in new ways.

Declarations

- Funding: This research did not receive any funding.
- Data availability: Data from the numerical simulations in this work can be accessed online: https://figshare.com/articles/dataset/_/31081768
- Code availability: Source code of numerical simulations will be made available on publication.

Appendix A Details of Simulated Annealing Algorithm to fit a Difference Neuron to an LIF Neuron

In one setup the LIF Neuron was calibrated to spike at 10.0 Hz by automatically adjusting the threshold, leaving the synaptic weights

unchanged, until the output frequency was matched (Figures A1a-A1c and A1g-A1i). In another experiment the LIF Neuron was adjusted in the same way, to respond at 100 Hz (Figures A1d-A1f and A1d-A1f). See Table C5 for a detailed parameter list.

To reduce the number of Difference Neuron parameters to be adapted, we set some parameters of the Difference Neurons to pre-defined values. The top and right border of an excitatory Sensitive Zone were fixed to 1.0 (no response delay, no gap detection), and the zone had a small fixed width (no bursting). Similarly, the inhibitory Sensitive Zone had a lower and a left border both fixed to -1.0 (no deactivation without new stimuli, no fast inhibition). The left, top, and bottom borders of the feedback zone were fixed to -1.0, 1.0, and -1.0, respectively (refractory period insensitive to response spike coincidences). Weights were fixed such that all Difference Detectors had to be active for the Difference Neuron to fire.

All neurons received spike-time identical realisations of Poisson distributed random stimulus. Mimicking the many low-rate connections to a natural neuron, we stimulated with several different fixed rates between 400 Hz and 1400 Hz. To achieve best fitting results we kept this rate static.

The Simulated Annealing minimizes a distance function that reflects the difference in spiking of a target neuron (the LIF Neuron) and a candidate Difference Neuron. It was calculated by adding a bounded squared difference of both neuron’s response ISI means and of both neurons response ISI variances:

$$C = \frac{1}{2} \left(1.0 - e^{-\left(\frac{\sigma^2(DN) - \sigma^2(IF)}{\sigma^2(IF)} \right)^2} \right) + \frac{1}{2} \left(1.0 - e^{-\left(\frac{\langle DN \rangle - \langle IF \rangle}{\langle IF \rangle} \right)^2} \right) \quad (A1)$$

where $\sigma^2(DN)$ is the inter-spike-interval variance of the candidate Difference Neuron, $\langle DN \rangle$ is the inter-spike-interval mean of the Difference Neuron, and $\sigma^2(IF)$ and $\langle IF \rangle$ are the same values for the LIF Neuron. Based on the assumption that very large errors are outside meaningful

adjustment by gradient descent, the exponential scaling dampens the effect of very large errors and increases the effect of small to medium sized differences. If the relative inter-spike interval mean and variance values of Difference and LIF Neurons are equal the cost is 0. If both differ by an infinite amount the cost is 1.0.

The classical Simulated Annealing algorithm starts with a random parameter setting and estimates a cost function. Then a slight random change to the parameters is made and the cost re-evaluated. If the changed parameter set has performed better than the previous, it is selected for the next trial, if it has performed worse, it may still be selected with a certain probability. If it has performed worse and is not selected, the next trial is done with the same parameter set. This probability is the “temperature” and is being reduced during the algorithm. Selecting parameter sets that perform worse helps to escape local minima.

A cost function that expresses the difference between a Difference Neuron and an LIF Neuron, based on a sample stimulus spike train and the two resulting response spike trains is an estimate of a theoretical cost. Early tests showed cost estimates to vary greatly for identical parameter sets but different stimuli. To be able to compare a next candidate parameter set to a previous parameter set, and still use different random stimuli for each trial to prevent over-fitting, we simulated the target LIF Neuron and two Difference Neurons instead of one Difference Neuron in each trial. One Difference Neuron is setup using the last parameter set, the other using the next candidate parameter set. That way a different random stimulus can be used for each trial. In each trial, all three neurons received the same stimulus and the first and second Difference Neurons’ responses were compared to the LIF Neuron’s response.

Subsequent tests showed that, due to the noise in the cost estimation, the algorithm got trapped in local minima. Frequently, at the end with a temperature of zero, a parameter set was chosen that performed better in the current trial,

but led to a higher cost in all subsequent trials with different stimuli. The randomness in the algorithm was a sum of the randomness from deciding probabilistically whether or not to accept the worse-performing next candidate, and the inherent randomness from the cost estimation. To reduce this total noise we eliminated the added noise in the decision making and utilised the inherent noise from the cost function estimate for the decision making instead. After calculating the cost estimate, the new candidate is always accepted if it has not performed worse by a certain value. That value was lowered during the run of the algorithm. This has the same effect as using a random probabilistic choice in a classical non-probabilistic cost scenario. Since longer simulation times decrease the estimation error, we could reduce the simulation length at the beginning of the algorithm, and increase it towards the end, achieving higher precision while getting the total time of the algorithm down to acceptable values (several days on a standard computer).

The Difference Neurons were each set up with one (stimulus) Difference Detector connected to an excitatory stimulus, and one (feedback) Difference Detector connected to the neuron’s own response. Weights for both detector’s zones were set to $w_i = 0.6$, both Difference Detectors are required to be active for the neuron to fire. The stimulus Difference Detectors of either neuron and the input for the LIF Neuron were fed the same stimulus, a Poisson sampled spike train with rate $\lambda_E = 500$ Hz. In a second setup we added an inhibitory Difference Detector to the neurons, connected to a Poisson sampled stimulus with a rate of $\lambda_I = 500$ Hz. Since the stimulus was static (a fixed expectation), dynamic Difference Neurons would have performed in the same way as the static Difference Neurons, therefore fitting a dynamic Difference Neuron was unnecessary.

Simulated annealing was performed for 5000 trials. At each trial, the response difference of the first Difference Neuron (using the winning parameters from the last trial) to the LIF Neuron was compared to the response difference of the

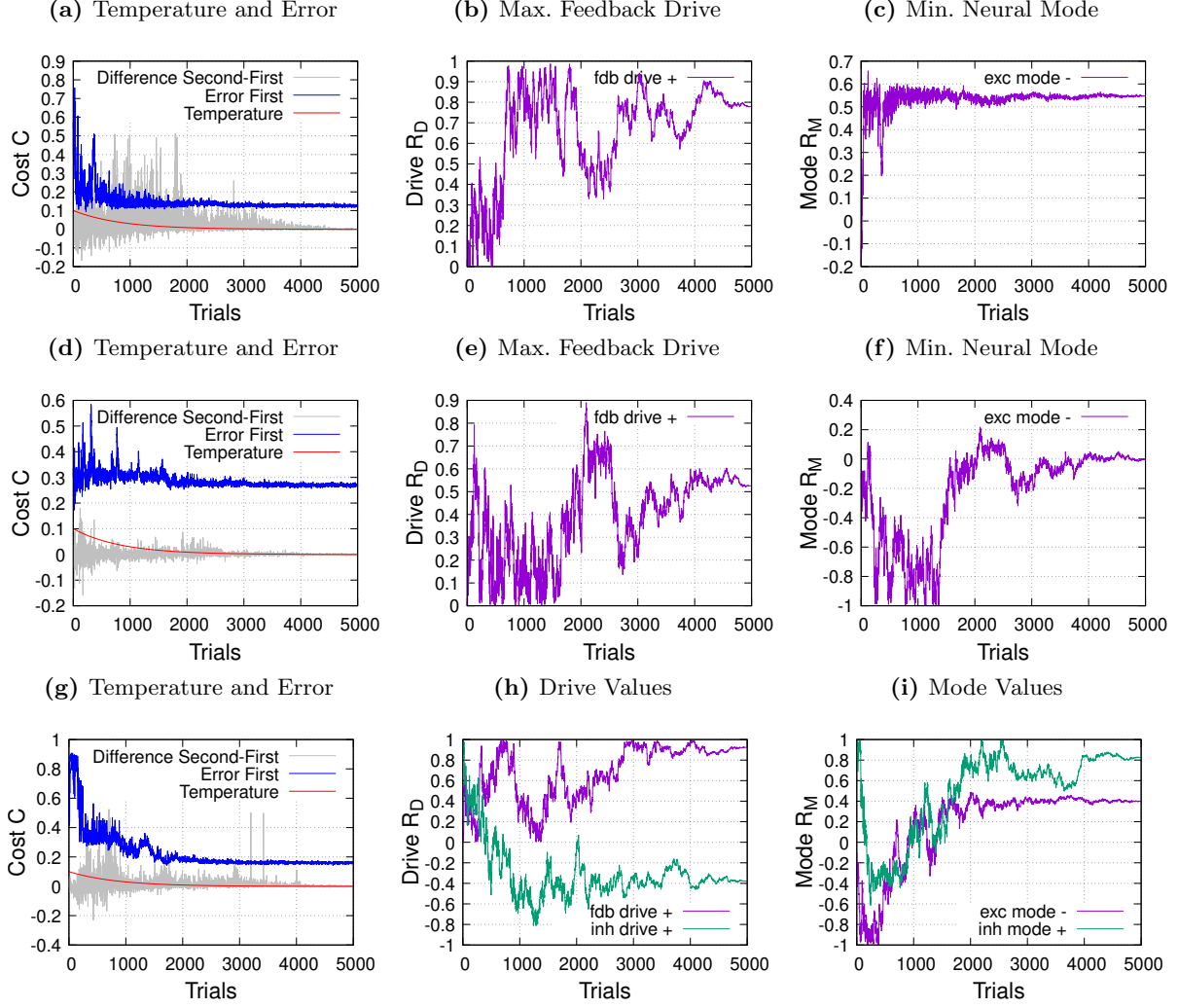


Fig. A1: Fitting a Difference Neuron to an LIF Neuron.

Time course of three Simulated Annealing trials to fit a Difference Neuron to different LIF Neurons.

Top row ((a), (b), (c)): A difference neuron is fitted to an LIF Neuron with low (10 Hz) response rate. Middle row ((d), (e), (f)): A Difference Neuron is fitted to an LIF Neuron with high response rate (100 Hz). Bottom row ((g), (h), (i)): A Difference Neuron is fitted to an LIF Neuron with two stimuli, excitatory and inhibitory, and a low response rate (10 Hz). Left column ((a), (d), (g)): The development of the temperature (red curves), the cost function C of the first Difference Neuron (equation A1) (blue curves), and the difference of the cost functions of both Difference Neurons (grey curves), during the fitting procedure. Middle column ((b), (e), (h)): The development of the upper neural drive border d^+ of the feedback Difference Detector (purple curves) and the inhibitory upper neural drive border (green curve) during fitting. Right column ((c), (f), (i)): The development of the excitatory stimulus Difference Detector's lower Neural Mode border m^- (purple curves) and the upper neural mode border m^+ of the inhibitory Difference Detector during fitting. For a detailed list of parameter values see Table C5.

second Difference Neuron (using the new candidate parameters) to the LIF Neuron. The neuron that performed better by a certain amount (the “temperature”) was used in the next step, with a new second neuron with parameters slightly and randomly different than the other. The value by which the second Difference Neuron was allowed

to perform worse and still be accepted (the temperature value) was 0.25 at the beginning, then decreased exponentially, down to -0.05 at the end of the algorithm. To prevent the algorithm converging to areas where the Difference Neuron does not respond at all, non-spiking parameter sets were discarded, and the step re-executed with a

new random candidate. Simulated Annealing cannot tell whether it has reached a global optimum. To keep the total calculation time within acceptable limits, instead of lengthening the algorithm further, the complete procedure was executed several times to fit a Difference Neuron to the same LIF Neuron parameter set, and the best result was chosen. A time course of the fitting procedure is shown in Figure A1, and the resulting optimal parameters are listed in Table C5.

We plotted temperature (red curves in Figures A1a, A1d, A1g), error (blue curves in the same plots) and the difference of both neuron's cost (grey curves). The development of the parameters during the fitting is shown in Figures A1h, A1i, A1e, A1f, A1b, A1c. When the second Difference Neuron performed worse than the first, the difference was negative (grey curve smaller than zero), when that difference was below the temperature (grey curve smaller than red curve) this worse parameter set was still accepted. During Simulated Annealing there are fewer and fewer cases where worse parameter sets occur (grey curve becoming positive) and are accepted (grey curve underneath red curve).

Appendix B Approximation of Synchronisation Measure

The authors (Golomb et al. 1992; Golomb and Rinzel 1993; Golomb et al. 1994; Ginzburg and Sompolinsky 1994) defined a synchrony measure $\chi(n)$ as the square root of the variance $\sigma_V^2 = \langle V_t^2 \rangle - \langle V_t \rangle^2$ of the average network voltage $V(t) = \frac{1}{n} \sum_i V_i(t)$ in a network with n neurons, divided by the average of the individual neuron voltage variances:

$$\chi^2(n) = \frac{\sigma_V^2}{\frac{1}{n} \sum_{i=1}^n \sigma_{V_i}^2}. \quad (\text{B2})$$

The approximation we use here is based on the assumption that all neurons in the network have identical response frequencies. Since the time

course of the activation Δ_i of a single neuron i in the network (defined in equation 6) consists of zeros and ones only,

$$\sigma_{\Delta_i}^2 = \langle \Delta_i^2 \rangle - \langle \Delta_i \rangle^2 = \langle \Delta_i \rangle - \langle \Delta_i \rangle^2.$$

When we estimated the network synchronisation, network activity plots showed the activity to be spread evenly across all neurons (figure 19). This justifies approximating a single neuron's mean $\langle \Delta_i \rangle$ by $\frac{1}{n}$ of the mean of the total network output $\langle \Delta \rangle = \langle \sum_i \Delta_i \rangle$,

$$\langle \Delta_i \rangle \approx \frac{1}{n} \langle \Delta \rangle,$$

so we can simplify the sum $\sum \sigma_{\Delta_i}^2$ of all single neuron variances by

$$\begin{aligned} \sum_{i=1}^n \sigma_{\Delta_i}^2 &= \sum_{i=1}^n \left(\langle \Delta_i \rangle - \langle \Delta_i \rangle^2 \right) \\ &\approx n \left(\frac{1}{n} \langle \Delta \rangle \right) - \sum_{i=1}^n \left(\frac{1}{n} \langle \Delta \rangle \right)^2 \\ &= \langle \Delta \rangle - \frac{1}{n} \langle \Delta \rangle^2. \end{aligned}$$

With this, the synchronisation measure becomes

$$\chi^2(n) = \frac{\frac{1}{n^2} \sigma_{\Delta}^2}{\frac{1}{n} \sum_{i=1}^n \sigma_{\Delta_i}^2} \approx \frac{\sigma_{\Delta}^2}{n \langle \Delta \rangle - \langle \Delta \rangle^2}, \quad (\text{B3})$$

where σ_{Δ}^2 is the variance of the total network activity Δ (note that σ_V^2 is the variance of a single neuron's voltage while σ_{Δ}^2 is the variance of the total network activity, hence the different factor $1/n$).

Appendix C Detailed Parameters of Simulations

Shown in Figures	Context	Parameter	Value
Default	Simulation	Time step per simulation	0.1 ms
		Simulated time	2000 s
		Number of simulations	200
	Stimulus	Type	Poisson distr. spikes
		Rate	10 Hz
	Stimulus Diff. Detector 1	Signal source	Stimulus
		w (weight)	0.6
		N (multiplicity)	1
		Static: Expected intervals r_0^*, r_N^*	1/10 s
		Dynamic: Estimation size M	50
	Feedback Diff. Detector	Signal source	Response
		w (weight)	0.6
		d^-, d^+, m^-, m^+ (zone borders)	-1, 0.8, -1, 1
		N (multiplicity)	1
		r_0^*, r_N^* (expected intervals)	1/10 s
4	Stimulus Diff. Detector	d^-, d^+, m^-, m^+ (zone borders) at start	0.9, 1, -1, -0.7
		d^-, d^+, m^-, m^+ (zone borders) at end	0.9, 1, 0.7, 1
6	Stimulus Diff. Detector	d^-, d^+, m^-, m^+ (zone borders) at start	-1, -0.9, -1, 1
		d^-, d^+, m^-, m^+ (zone borders) at end	0.9, 1, -1, 1

Table C1: Difference Neuron Parameters for the Single-Stimulus Parameter Scans shown in Figures 4 and 6.

Figures	Context	Parameter	Value
Default	Simulation	Time step	0.1 ms
		Length	1 s
	Stimulus	Type	Poisson distr. spikes
		Rate	10 Hz
	Stimulus Diff. Detector	Signal source	Stimulus
		d^-, d^+, m^-, m^+ (zone borders)	0.95, 1, 0.5, 1
		w (weight)	0.6
		N (multiplicity)	1
		r_0^*, r_N^* (expected intervals)	1/10 s
	Feedback Diff. Detector	Signal source	Response
		w (weight)	0.6
		d^-, d^+, m^-, m^+ (zone borders)	-1, 0.9, -1, 1
		N (multiplicity)	1
		r_0^*, r_N^* (expected intervals)	1/10 s
7a, 7b	Stimulus	Type	Poisson spike train plus regular repetitions
		Rate	20 Hz
	Stimulus Diff. Detector	d^-, m^- (zone borders)	-1, 0.75
		r_0^*, r_N^* (expected intervals)	1/20 s
	Feedback Diff. Detector	d^+ (zone border)	0.8
3a, 3b	Stimulus Diff. Detector	m^-, m^+ (zone borders)	0.5, 1
3c, 3d	Stimulus Diff. Detector	m^-, m^+ (zone borders)	-1, -0.5
5c, 5d	Stimulus Diff. Detector	d^-, d^+ (zone borders)	0.45, 0.5
5e, 5f	Stimulus Diff. Detector	d^-, d^+ (zone borders)	-0.05, 0
7c, 7d	Stimulus Diff. Detector	d^-, m^- (zone borders)	-0.5, 0.5
8c	Stimulus Diff. Detector	N (multiplicity)	3
8d	Stimulus Diff. Detector	N (multiplicity)	5

Table C2: Difference Neuron Parameters for the Single-Stimulus Examples shown in Figures 3, 5, 7 and 8.

Shown in Figures	Context	Parameter	Value
Default	Simulation	Time step	0.1 ms
		Length	1 s
	Stimulus 1	Type	Poisson distr. spikes
	Stimulus 2	Type	Poisson distr. spikes
	Stimulus Diff. Detector 1	Signal source	Stimulus 1
		w (weight)	0.4
		N (multiplicity)	1
	Stimulus Diff. Detector 2	Signal source	Stimulus 2
		w (weight)	0.4
		N (multiplicity)	1
	Response Diff. Detector	Signal source	Response
		w (weight)	0.4
		N (multiplicity)	1
		d^-, d^+, m^-, m^+ (zone borders)	-1, 0.5, -1, 1
9a, 9b	Stimulus 1	Rate	20 Hz
	Stimulus Diff. Detector 1	d^-, d^+, m^-, m^+ (zone borders)	0.8, 1, 0.5, 1
		r_0^*, r_N^* (expected intervals)	1/20 s
	Stimulus 2	Rate	10 Hz
	Stimulus Diff. Detector 2	d^-, d^+, m^-, m^+ (zone borders)	-1, -0.1, -1, 1
		r_0^*, r_N^* (expected intervals)	1/10 s
9c, 9d, 9e, 9f	Response Diff. Detector	r_0^*, r_N^* (expected intervals)	1/10 s
	Stimulus 1	Rate	25 Hz
	Stimulus Diff. Detector 1	d^-, d^+, m^-, m^+ (zone borders)	0.8, 1, -1, 1
		r_0^*, r_N^* (expected intervals)	1/25 s
	Stimulus 2	Rate	27 Hz
	Stimulus Diff. Detector 2	r_0^*, r_N^* (expected intervals)	1/27 s
9c, 9d	Response Diff. Detector	r_0^*, r_N^* (expected intervals)	1/26 s
	Stimulus Diff. Detector 2	d^-, d^+, m^-, m^+ (zone borders)	0.81, 1.01, -1, 1
9e, 9f	Stimulus Diff. Detector 2	d^-, d^+, m^-, m^+ (zone borders)	0.55, 0.75, -1, 1

Table C3: Difference Neuron Parameters for the Dual-Stimulus Examples shown in Figure 9.

Shown in Figures	Context	Parameter	Value
Default	Simulation	Time step dt	0.05 ms
	Network	Number of Neurons	250
		Connection probability	0.1
	Excitatory stimulus N_t^E	Type	Poisson distr. spikes
		Rate	1 Hz
	Stimulus Diff. Detector	Signal source	Sum of pre-synaptic neurons and excitatory stimulus
		r_0^*, r_N^* (expected intervals)	1/10 s
		N (multiplicity)	1
	Feedback Diff. Detector	Signal source	Response
		r_0^*, r_N^* (expected intervals)	1/10 s
		N (multiplicity)	1
		d^-, d^+, m^-, m^+ (zone borders)	-1.0, 0.0, -1.0, 1.0
10, 12, 13	Simulation	Simulated time	200 s
14	Simulation	Simulated time	10 intervals of 5 s
10	Stimulus Diff. Detector 1	d^-, d^+, m^-, m^+ (zone borders)	-1.0, -0.9, -1.0, -0.5
12	Stimulus Diff. Detector 1	d^-, d^+, m^-, m^+ (zone borders)	0.08, 0.1, 0.5, 1.0
13	Stimulus Diff. Detector 1	d^-, d^+, m^-, m^+ (zone borders)	-1.0, -0.9, -1.0, -0.5

Table C4: Parameters for the Difference Neuron network in Figures 10, 12, 13 and 14.

Shown in Figures	Context	Parameter	Value
Default	Simulation	Time step dt	0.01 ms
	Excitatory stimulus N_t^E	Rate	500 Hz
	LIF Neuron excitatory conductance	driving process G_t^E	N_t^E
		rev. pot. v_E	10 mV
		weight w_E	0.2
	LIF Neuron leak conductance	driving process G_t^L	t
		rev. pot. v_L	-50 mV
		weight w_L	1 / 20 ms
	LIF Neuron membrane	time const $1/w_L$	20 ms
		reset value V_0	-70 ms
15a, 15b, A1a, A1b, A1c	Stimulus Diff. Detector 1	Signal source	Excitatory stimulus
		d^-, d^+, m^+ (zone borders)	0.9, 1.0, 1.0
		r_0^*, r_N^* (expected intervals)	1/500 s
		N (multiplicity)	6
	Feedback Diff. Detector	Signal source	Response
15c, 15d, A1d, A1e, A1f	Stimulus Diff. Detector 1	d^-, d^+, m^+ (zone borders)	-1.0, -1.0, 1.0
		r_0^*, r_N^* (expected intervals)	1/10 s
		N (multiplicity)	1
		d^+ (zone border)	0.778954
	Feedback Diff. Detector	r_0^*, r_N^* (expected intervals)	1/10 s
16a, 16b, A1g, A1h, A1i	Stimulus Diff. Detector 1	C (error after fitting)	0.120744
		v_θ (spiking threshold)	1.01784 mV
		Response rate	10 Hz
		m^- (zone border)	0.547095
	Feedback Diff. Detector	d^+ (zone border)	0.778954
16a, 16b, A1g, A1h, A1i	Stimulus Diff. Detector 1	r_0^*, r_N^* (expected intervals)	1/10 s
		C (error after fitting)	0.266871
		v_θ (spiking threshold)	-22.2525 mV
		response rate	100 Hz
	Stimulus Diff. Detector 1	m^- (zone border)	-0.00389221
		d^+ (zone border)	0.525162
		r_0^*, r_N^* (expected intervals)	1/100 s
		C (error after fitting)	0.158358
	LIF Neuron inhibitory conductance	Rate	500 Hz
		v_θ (spiking threshold)	-6.61022 mV
		Response rate	10 Hz
16a, 16b, A1g, A1h, A1i	LIF Neuron inhibitory conductance	driving process G_t^I	N_t^I
		rev. pot. v_I	-70 mV
		weight w_I	0.2
	Stimulus Diff. Detector 1	m^- (zone border)	0.398298
		Signal source	Inhibitory stimulus
	Stimulus Diff. Detector 2	d^-, m^- (zone borders)	-1.0, -1.0
		d^+, m^+ (zone borders)	-0.377711, 0.826508
		r_0^*, r_N^* (expected intervals)	1/500 s
		N (multiplicity)	6
	Feedback Diff. Detector	d^+ (zone border)	0.923063
		r_0^*, r_N^* (expected intervals)	1/10 s

Table C5: Parameters for LIF Neuron vs. Difference Neuron Comparison Examples shown in Figures 15, 16 and A1.

Shown in Figures	Context	Parameter	Value
Default	Simulation	Time step dt	0.01 ms
	Excitatory stimulus N_t^E	Rate	400 Hz – 1400 Hz
	LIF Neuron excitatory conductance	driving proces G_t^E	N_t^E
		rev. pot. v_E	10 mV
		weight w_E	0.2
	LIF Neuron leak conductance	driving process G_t^L	t
		rev. pot. v_L	-50 mV
		weight w_L	1 / 20 ms
	LIF Neuron membrane	time const $1/w_L$	20 ms
		reset value V_0	-70 ms
		Spiking threshold v_θ	1.018 mV
	Diff. Detector 1	Signal source	Excitatory stimulus
		Drive borders d^-, d^+	0.9, 1.0
		Mode borders m^-, m^+	0.547, 1.0
		N (multiplicity)	6
17	Static Stimulus Diff. Detector	r_0^*, r_N^* (expected intervals)	1/500 s
	Dynamic Stimulus Diff. Detector	Estimation size M	100
	Feedback Diff. Detector	Signal source	Response
		Drive borders d^-, d^+	-1.0, 0.779
		Mode borders m^-, m^+	-1.0, 1.0
		r_0^*, r_N^* (expected intervals)	1/10 s
		N (multiplicity)	1
	Simulation	data points per plot	200
		Simulated time	500 s
18	Simulation	Data points per plot	1
		Simulated time	5000 s

Table C6: Parameters for the LIF Neuron regime-change comparison in Figures 17 and 18.

Shown in Figures	Context	Parameter	Value
Default	Simulation	Time step dt	0.05 ms
		Connection probability	10%
		Stimulus	Sum of responses of connected neurons, plus external stimulus
	All networks	Number of neurons	100
	All Difference Neurons	Stimulus Diff. Detector (SDD)	connected to stimulus
		SDD d^-, d^+ (drive borders)	0.9, 1.0
		SDD m^-, m^+ (mode borders)	0.547, 1.0
		SDD N (multiplicity)	6
		Feedback Diff. Detector 2 (FDD)	connected to response
		FDD d^-, d^+ (drive borders)	-1.0, 0.779
		FDD m^-, m^+ (mode borders)	-1.0, 1.0
		FDD r_0^*, r_N^* (expected intervals)	1/10 s
		FDD N (multiplicity)	1
	Static Diff. Neurons	SDD r_0^*, r_N^* (expected intervals)	1/500 s
	Dynamic Diff. Neurons	SDD M (stimulation size)	100
	LIF Neurons	v_θ (spiking threshold)	0.646 mV
		V_0 (reset voltage)	-70 mV
		v_L (leak potential)	-50 mV
		$1/w_L$ (membrane time constant)	20 ms
		Spike height	20 mV
		v_E (exc. reversal potential)	10 mV
		w_E (exc. weight)	0.2
19	Simulation	Total simulated time	4 s
		Pre-run interval	0.3 s
19a	Simulation	Stimulus rate	460 Hz
19b	Simulation	Stimulus rate (high)	600 Hz
		Stimulus rate (low)	300 Hz
		Total high-stimulation time	2×0.5 s
20	Simulation	Simulations per plot	3000
		Simulated time per simulation	5 s
		Simulations per frequency	36
		Rate resolution	0.1 Hz

Table C7: Parameters for Network Comparison Test in Figures 19 and 20.

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