Introduction to spiking neural networks: Information processing, learning and applications

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The concept that neural information is encoded in the firing rate of neurons has been the dominant paradigm in neurobiology for many years. This paradigm has also been adopted by the theory of artificial neural networks. Recent physiological experiments demonstrate, however, that in many parts of the nervous system, neural code is founded on the timing of individual action potentials. This finding has given rise to the emergence of a new class of neural models, called spiking neural networks. In this paper we summarize basic properties of spiking neurons and spiking networks. Our focus is, specifically, on models of spike-based information coding, synaptic plasticity and learning. We also survey real-life applications of spiking models. The paper is meant to be an introduction to spiking neural networks for scientists from various disciplines interested in spike-based neural processing.

Key words: neural code, neural information processing, reinforcement learning, spiking neural networks, supervised learning, synaptic plasticity, unsupervised learning

INTRODUCTION

Spiking neural networks (SNN) represent a special class of artificial neural networks (ANN), where neuron models communicate by sequences of spikes. Networks composed of spiking neurons are able to process substantial amount of data using a relatively small number of spikes (VanRullen et al. 2005). Due to their functional similarity to biological neurons, spiking models provide powerful tools for analysis of elementary processes in the brain, including neural information processing, plasticity and learning. At the same time spiking networks offer solutions to a broad range of specific problems in applied engineering, such as fast signal-processing, event detection, classification, speech recognition, spatial navigation or motor control. It has been demonstrated that SNN can be applied not only to all problems solvable by non-spiking neural networks, but that spiking models are in fact computationally more powerful than perceptrons and sigmoidal

gates (Maass 1997). Due to all these reasons SNN are the subject of constantly growing interest of scientists.

In this paper we introduce and discuss basic concepts related to the theory of spiking neuron models. Our focus is on mechanisms of spike-based information processing, adaptation and learning. We survey various synaptic plasticity rules used in SNN and discuss their properties in the context of the classical categories of machine learning, that is: supervised, unsupervised and reinforcement learning. We also present an overview of successful applications of spiking neurons to various fields, ranging from neurobiology to engineering. Our paper is supplemented with a comprehensive list of pointers to literature on spiking neural networks.

The aim of our work is to introduce spiking neural networks to the broader scientific community. We believe the paper will be useful for researchers working in the field of machine learning and interested in biomimetic neural algorithms for fast information processing and learning. Our work will provide them with a survey of such mechanisms and examples of applications where they have been used. Similarly, neuroscientists with a biological background may find the

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paper useful for understanding biological learning in the context of machine learning theory. Finally, this paper will serve as an introduction to the theory and practice of spiking neural networks for all researchers interested in understanding the principles of spike-based neural processing.

SPIKING MODELS

Biological neurons communicate by generating and propagating electrical pulses called action potentials or spikes (du Bois-Reymond 1848, Schuetze 1983, Kandel et al. 1991). This feature of real neurons became a central paradigm of a theory of spiking neural models. From the conceptual point of view, all spiking models share the following common properties with their biological counterparts: (1) They process information coming from many inputs and produce single spiking output signals; (2) Their probability of firing (generating a spike) is increased by excitatory inputs and decreased by inhibitory inputs; (3) Their dynamics is characterized by at least one state variable; when the internal variables of the model reach a certain state, the model is supposed to generate one or mores spikes.

The basic assumption underlying the implementation of most of spiking neuron models is that it is timing of spikes rather than the specific shape of spikes that carries neural information (Gerstner and Kistler 2002b). In mathematical terms a sequence of the firing times - a spike train - can be described as $S(t)=\sum_f \delta(t-t^f)$,

where $f = 1, 2, ...$ is the label of the spike and $\delta(.)$ is a Dirac function with $\delta(t)\neq 0$ for t=0 and $\int_{-\infty}^{\infty}\delta(t)dt=1$.

Historically the most common spiking neuron models are Integrate-and-Fire (IF) and Leaky-Integrate-and-Fire (LIF) units (Lapicque 1907, Stein 1967, Gerstner and Kistler 2002b). Both models treat biological neurons as point dynamical systems. Accordingly, the properties of biological neurons related to their spatial structure are neglected in the models. The dynamics of the LIF unit is described by the following formula:

$$C\frac{\mathrm{d}u}{\mathrm{d}t}(t) = -\frac{1}{R}u(t) + \left(i_o(t) + \sum w_j i_j(t)\right), \qquad (1)$$

where u(t) is the model state variable (corresponding to the neural membrane potential), C is the membrane capacitance, R is the input resistance, $i_o(t)$ is the external current driving the neural state, $i_j(t)$ is the input current from the j-th synaptic input, and w_j represents the strength of the j-th synapse. For R→∞, formula (1) describes the IF model. In both, IF and LIF models, a neuron is supposed to fire a spike at time tf , whenever the membrane potential u reaches a certain value υ called a firing threshold. Immediately after a spike the neuron state is reset to a new value u_{res}<υ and hold at that level for the time interval representing the neural absolute refractory period (Fig. 1).

Neurons connect and communicate with one another through specialized junctions called synapses
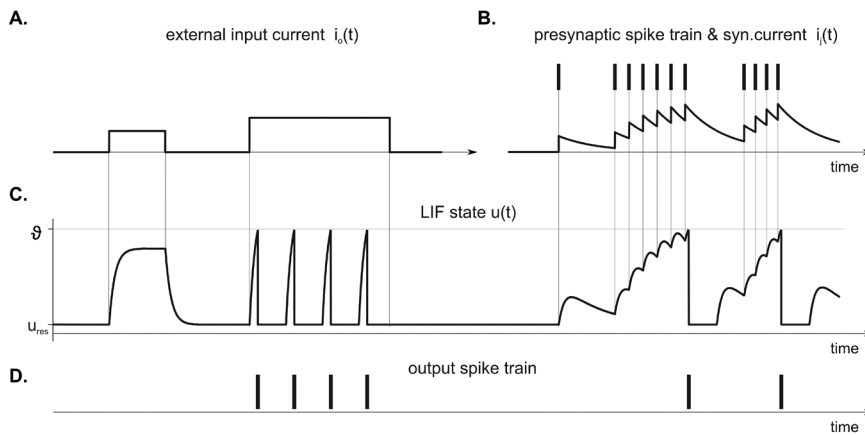

Fig. 1. Time course of the membrane potential u(t) of a leaky-integrate-and-fire neuron LIF (panel C) driven by the external input current $i_o(t)$ (shown in panel A) or by the synaptic current i_j (t) evoked by the sample presynaptic spike train (panel B). Initially, the state u(t) of the LIF neuron is at the resting value u_{res}. The currents $i_o(t)$ and $i_j(t)$ increase the membrane potential towards the firing threshold θ. Whenever the threshold is crossed the neuron emits a spike and the membrane voltage u(t) is reset to a new value - here assumed u_{res}. The firing times of the LIF neuron are shown as vertical bars in panel D.

(Sherrington 1897, Bennett 1999). Arrival of a presynaptic spike at a synapse triggers an input signal i(t) into the postsynaptic neuron. This signal corresponds to the synaptic electric current flowing into the biological neuron (Kandel et al. 1991). In a simple model the time course of i(t) can be described by the exponential function:

$$i(t) = \int_0^\infty S_j(s-t) \exp(-s/\tau_s)\, \mathrm{d}s, \qquad (2)$$

where τ_s is the synaptic time constant and $S_j(t)$ denotes a presynaptic spike train. A typical response of the synapse model given by (2) to a sample input spike train is illustrated in Fig. 1 (top right plot). For an excellent review of spiking neuron models we refer the reader to Gerstner and Kistler (2002b).

Given the models of neurons and synapses we can define a spiking neural network. Typically an SNN is considered as a finite directed graph (V, E), with V being a set of neurons and E representing a set of synapses (Maass 1996). In particular the set V contains a subset of input neurons V_{in} and a subset of output neurons V_{out}. The firing of input neurons is assumed to be determined from outside of the SNN, that is the sets of firing times – for the neurons in V_{in} are given as the input of the SNN.

Spiking network topologies can be classified into three general categories:

1. Feedforward networks – this is where the data flow from input to output units is strictly one-directional; the data processing can extend over multiple layers of neurons, but no feedback connections are present. In biological neural systems feedforward projections can be found mainly in areas closer to the periphery. Similarly, in SNN feedforward topologies are usually applied to model low-level sensory systems, e.g. in vision (Perrinet et al. 2004, Escobar et al. 2009), olfaction (Rochel et al. 2002) or tactile sensing (Cassidy and Ekanayake 2006). Feedforward networks are investigated also in the context of spike synchronization (Kumar et al. 2010) or for solving the binding problem based on spatio-temporal patterns of spikes (Natschlaeger 1999).

2. Recurrent networks – here individual neurons or populations of neurons interact through reciprocal (feedback) connections. Feedback connections result in an internal state of the network which allows it to exhibit dynamic temporal behavior. Consequently recurrent networks are characterized by richer dynamics and potentially higher computational capabilities than feedforward networks. Unfortunately, they are also more difficult to control and train (Hertz et al. 1991). Recurrent spiking neural networks have been used e.g. to investigate neural information processing involved in formation of associative memories (Gerstner and van Hemmen 1992, Sommer and Wennekers 2001, Zamani et al. 2010) or working memory (Amit and Mongillo 2003, Mongillo et al. 2008, Szatmary and Izhikevich 2010). Spiking networks with recurrent connections have also been used to model and analyze phenomena observed in the brain that emerge from complex dynamics of reciprocal interactions, such as network oscillations (Buzsaki 2006, Izhikevich and Edelman 2008, Melamed et al. 2008) or network multistability (Ma and Wu 2007). Networks with lateral inhibitory interactions are often used for signal decorrelation (Linster and Cleland 2010, Tkacik et al. 2010) or to implement competition between neurons or neural populations (Lumer 2000, Jin and Seung 2002), and thus are considered in the context of decision making (Wang 2008).

3. Hybrid networks – this group encompasses networks in which some subpopulations may be strictly feedforward, while other have recurrent topologies. Interactions between the subpopulations may be one-directional or reciprocal. Whereas multiple hybrid network architectures are possible, here we describe only two, probably the most extensively studied classes of hybrid spiking neural networks:

• Synfire chain – human learning often consists in associating two events, or linking a signal and a subsequent action into a causal relationship. The events are often separated in time but, nonetheless, humans can link them, thereby allowing them to accurately predict the right moment for a particular action. Synfire chain is considered as a possible mechanism for representing such relationships between delayed events (Abeles 1982). Synfire chain is a multi-layered architecture (a chain), in which spiking activity can propagate as a synchronous wave of neuronal firing (a pulse packet) from one layer (subpopulation) of the chain to the successive ones (Diesmann et al. 1999). This definition suggests a feedforward architecture, however, the particular subpopulations may contain recurrent connections. An excellent review of synfire chain mechanisms and properties is provided in Kumar and coauthors article (2010).

• Reservoir computing – is a computational concept that takes advantage of properties of recurrent networks, while avoiding difficulties associated with their training (Atiya and Parlos 2000, Dominey and Ramus 2000, Jaeger 2001, Maas et al. 2002a, Schrauwen et al. 2007, Lukosevicius and Jaeger 2009). In a typical implementation a reservoir network consists of a fixed recurrent structure (a reservoir) and a set of output neurons called readouts. Usually, readouts receive only feedforward connections from the reservoir, although a feedback from readouts to the reservoir is also considered in some models. Nevertheless, the desired output from the network is obtained by training only the connections from the reservoir neurons to readout neurons. Such an approach highly simplifies training in reservoir networks.

Reservoir can be viewed as a structure performing the mapping from inputs onto a high-dimensional vector of an activity of neurons belonging to the network. Each component of this vector reflects the impact that the particular neurons may have on the output units. The connectivity structure within the reservoir is usually random and fixed (although, it has been shown that some adaptivity within a reservoir may facilitate the task of an output neuron for a family of related tasks, see e.g. Häusler et al. 2003). Stable internal states of the reservoir are not necessary for producing stable outputs, since transient internal states can be transformed by readout neurons into stable target outputs making use of the high dimensionality of the dynamical system (Maass et al. 2002a). Moreover, the reservoir states and the transitions between them need not be customized for a specific task. It means that the same, sufficiently large, generic reservoir can be used to perform many, different tasks (Maass et al. 2004).

The concept of reservoir computing has initially been suggested in the context of non-spiking ANN (Atiya and Parlos 2000, Dominey and Ramus 2000, Jaeger 2001, Steil 2004). More recently it has been adopted for spiking networks e.g. within the Liquid State Machine framework (Maass et al. 2002a,2003, Häusler et al. 2003). Reservoir computing with spiking units has so far been successfully applied to such tasks as: spoken-word recognition (Maass et al. 2003, Verstraeten et al. 2005), spatio-temporal spike pattern classification (Maass et al. 2002a, Ponulak and Kasinski 2010), motion prediction (Maass et al. 2002b) or motor pattern generation and motor control (Joshi and Maass 2005, Burgsteiner 2005, Belter et

al. 2008, Ponulak et al. 2008). More details on the particular tasks are presented in this paper in the 'Applications' section.

INFORMATION PROCESSING IN SPIKING NEURONS

Each millisecond, thousands of spikes emitted by sensory neurons are processed by the brain, which decides what actions are the most appropriate for the sensed stimuli. Sometimes decisions are made already within tens of milliseconds (VanRullen and Thorpe 2001, Girard et al. 2008). It is intriguing, what processes enable such a fast information processing. How is information encoded in the neural signals? What is the temporal resolution of signals required to perform precise computations?

These questions concerning the neural representation of information are often referred to as a problem of the neural code (Rieke et al. 1997). Here we review various hypotheses on the neural code and present them in the light of the recent neurophysiological findings on information processing mechanisms in the nervous system in animals.

In 1926, Adrian and Zotterman demonstrated that frog cutaneous receptors responded with more spikes whenever the strength of the external mechanical pressure on the frog skin increased. This finding gave rise to the idea that the neural information is encoded in the firing rate. The rate code has been a dominant paradigm in neurophysiology and artificial neural networks for many years. Recent neurophysiological results, however, suggest that, at least in some neural systems, efficient processing of information is more likely to be based on the precise timing of action potentials rather than on their firing rate (Lestienne 2001, Bohte 2004, Stein et al. 2005, Faisal et al. 2008, Tiesinga et al. 2008). The primary observation used as an argument against the rate code is that many behavioral responses are completed too quickly for the underlying sensory processes to rely on the estimation of neural firing rates over extended time windows (VanRullen et al. 2005)[1]. Another argument is that the rate, at which neurons fire, does not fully capture the information content conveyed in the spike-train. For example, it has been found that the populations of neurons in the primary auditory cortex can coordinate the relative timing of their action potentials by

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[1] However, for alternative theories supporting rapid information encoding/decoding based on the rate-code see Shadlen and Newsome (1998) and Huys and colleagues (2007).

grouping the neighboring spikes in short bursts, without changing the number of firings per second (deCharms 1998). This way, the neurons can signal stimuli even when their average firing rates do not change.

Evidence for the reproducibility of neural responses to the given stimuli with high precision of the order 0.2–2 ms was found in blowfly's visual cortex (de Ruyter van Steveninck et al. 1997), in cat's lateral geniculate nucleus (Liu et al. 2001), in the middle temporal area of the macaque (Bair and Koch 1996) or in the rabbit retina (Berry et al. 1997). Similar results on the reliable precision (2–3 ms) of single spikes have been reported for spinal neurons in the neonatal rat spinal cord (Beierholm et al. 2001). In bats and weakly electric fish, relative timing of spikes in multiple cells allows for the reliable discrimination of the time intervals of the order of 10^{-8} second, in spite of the fact that individual spikes have a duration of the order of 10^{-3} second. A population of nerve cells can therefore encode information that would otherwise be outside the limited bandwidth and resolution set by the maximal firing rate and action potential duration in individual neurons (Gabbiani and Midtgaard 2001).

Many experimental results on the neural code point out particularly to the high importance of each individual spike in the biological neural signals. In humans, precise timing of already first spikes in tactile afferents encodes touch signals at the finger tips (Johansson and Birznieks 2004). In cats and toads, a few retinal ganglion cells seem to encode information about light stimuli by firing only two or three spikes in about 100 ms under low light conditions (Gabbiani and Midtgaard 2001). This evidence suggests that in almost any system where the processing-speed of a neural system is required to be high, the timing of individual spikes carry important information.

Precise temporal coding paradigm is required also in some artificial control systems. Examples are neuro-prosthetic systems using electrical stimulation (ES) for producing functionally useful movements of the paralyzed limbs (Popovic and Sinkjaer 2000). These systems explore the fact that trains of short electrical pulses applied to nerves or muscles result in muscle contraction. Traditionally, movement control in the ES systems has been realized by modulating frequency or width of the electrical pulses. Several results, however, suggest that precise relative timing of stimulating pulses may be more effective in generating desired, smooth movement trajectories than the frequency modulation. One recently explored approach is to use ES not only to evoke direct muscle contraction, but also to trigger motor reflexes aiming at supporting a desired movement (Mulder et al. 1990, Sayenko et al. 2007). In this case the reflexes have specific temporal patterns and arrive within a time window of 50–100 ms after the initial stimulation, which puts certain limits on the number of stimulating pulses that can be delivered to the biological tissue to evoke a reflex, and thus it emphasizes the role of individual pulses and their timing in the ES.

The phenomena discussed here demonstrate the importance of analysis of the neural information processing, both in biological and in artificial systems, with focus on the timing of individual spikes/pulses. To address this problem several neural coding strategies based on spike timing have been proposed. In the following we shortly describe some of these strategies:

1. Time to first spike – in this model information in the neural systems is encoded in the latency between the beginning of stimulus and the time of the first spike in the neural response (Fig. 2A). Time to first spike has been shown to carry enough information e.g. to encode touch signals at the finger tips in the tactile system (Johansson and Birznieks 2004). Interesting enough, Saal and coauthors (2009) have shown that the first spikes provide more than twice the information about the stimulus shape present in the firing rate during a tactile stimulus discrimination task and similar amount of information about force direction as present in spike counts.

Time-to-first-spike scheme enables ultra-fast information processing, as a decision on a stimulus can be communicated by the arrival of the first spike already within a few milliseconds. The code is also very simple and can be implemented using just one neuron with inhibitory feedback interactions that prevent emission of all but the first spike. Time-to-first-spike model has been considered for input discrimination e.g. in artificial tactile and olfactory sensors (Kim et al. 2010, Chen et al. 2011).

2. Rank-order coding (ROC) – is another simple neural coding scheme. Here information is encoded by the order of spikes in the activity of a neural population (Fig. 2B). ROC approach has been proposed to explain ultra-fast categorization observed in the primate's visual system. Thorpe and colleagues (Thorpe 1990, VanRullen and Thorpe 2001) proposed that the order in which each ganglion cell emits its first spike codes for the visual stimulus. The ROC model assumes that each neuron emits only a single spike during a presentation of the image. This can be easily implemented in a feedforward

network with inhibitory feedback connections. Based on these principles and using the ROC approach, Thorpe and others (1997, 2001) developed a spiking neural model able to categorize static images with a processing speed comparable to that observed in humans.

3. Latency code – in this model information is supposed to be contained in the exact timing of a set of spikes relative to each other (Fig. 2C). As discussed before, precisely timed patterns of spikes have been postulated to play an important role in the nervous system in many functions (Bohte 2004). Precise relative spike timing is one of the critical parameters that control many forms of synaptic plasticity. Changing the relative timing of presynaptic and postsynaptic

spikes in a cortical neuron by as little as 10 ms can determine whether a synapse is potentiated or depressed (Markram et al. 1997). Latency code is also very efficient in terms of information capacity – timing of just a few spikes can carry a substantial amount of information (Borst and Theunissen 1999). Precisely timed sequences of spikes are typically observed in feedforward networks, since noise and inherent dynamics of recurrent networks can easily disrupt spike timing precision (Lestienne 2001, Faisal et al. 2008). Yet, some attempts to harvest precise spiking timing in recurrent networks have been made for example by exploring the idea of reservoir computation (Maass et al. 2002a, Ponulak and Kasinski 2010).
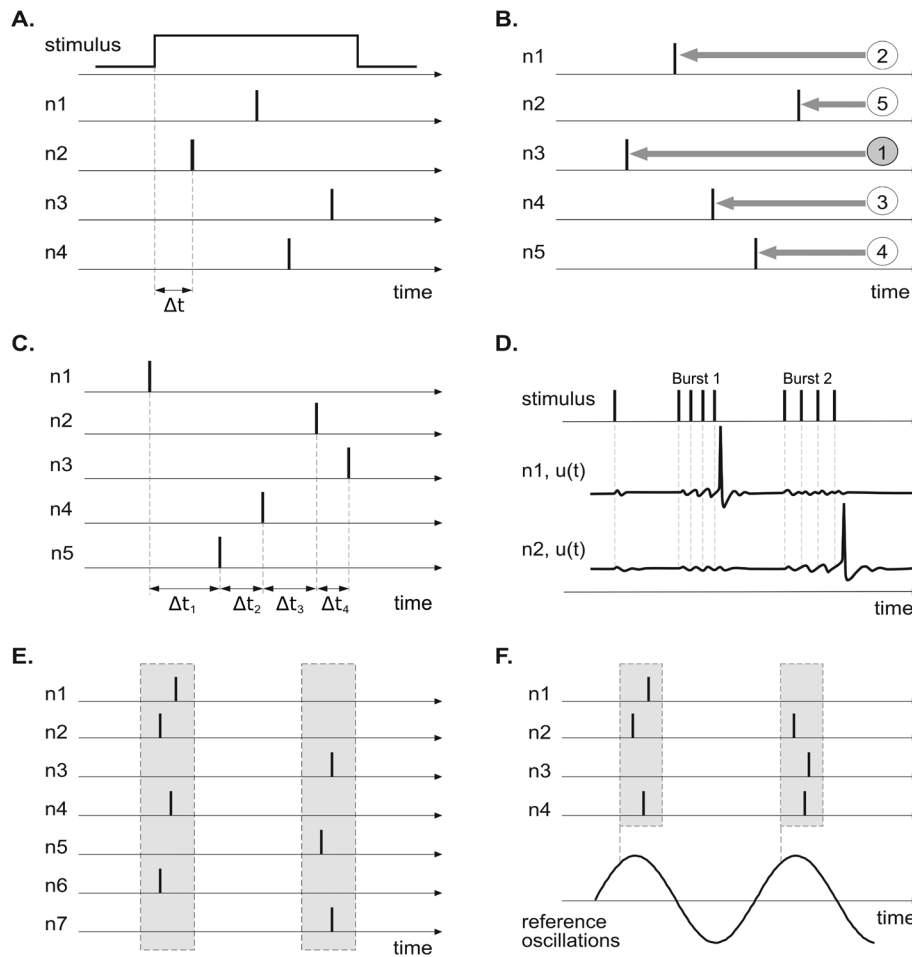

Fig. 2. Spike-based information coding strategies (see text for details): (A) time to first spike; (B) rank-coding or spike-order coding; (C) latency coding based on the exact timing of spikes; (D) resonant burst coding; (E) coding by synchrony; (F) phase coding. Legend: n1,...,n7 are the labels of neurons; the vertical bars in the particular plots represent the neural firing times; the numbers 1,...,5 in the circles indicate the order of spike arrival; Δt is the latency between the stimulus onset and the first spike; $\Delta t_1,...,\Delta t_4$ are the inter-spike latencies; $u(t)$ is the neuron model state variable.

4. Resonant burst model – in (Izhikevich 2002) it has been suggested that the frequency of a burst of spikes can determine which downstream neurons are activated. Using the resonance phenomenon, Izhikevich demonstrated that a short burst can elicit strong post-synaptic response if the burst frequency is tuned to the eigen-frequencies of the membrane potential oscillations in the target neurons. The same burst would have a negligible effect on the postsynaptic membrane potential if the burst and eigen-frequencies are not tuned (Fig. 2D). The author suggests that this phenomenon may provide an effective mechanism for selective communication between neurons.

5. Coding by synchrony – this model is based on the assumption that neurons that encode different bits of information on the same object fire synchronously (Fig. 2E). This concept is grounded on several experimental observations. For example, it has been shown that neurons in the visual cortex tend to synchronize their discharges with a precision in the millisecond range when activated with a single contour (Gray and Singer 1989), whereas they fail to do so when activated by different contours moving in different directions (Gray et al. 1989). It has also been suggested that synchronous firing of neurons in a population can carry information about the global significance of the stimulus for the animal (Gray et al. 1989) or to organize information together in packets (Jefferys et al. 1996). In principle, neuronal synchronization will serve as a mechanism improving, both information transmission through the network, as well as timing precision of spiking events (von der Malsburg 1985, Abeles et al. 1994, Singer 1999).

Synchronization has been investigated in the context of networks with dominant feedforward connections, such as in synfire chain networks, but synchronies events may also dynamically emerge in recurrent networks (Diesmann et al. 1999). In fact, synchronization can be established very rapidly – simulations demonstrate that networks of reciprocally coupled spiking neurons can undergo very rapid transitions from uncorrelated to synchronized states (e.g. Bauer 1993, Gerstner and van Hemmen 1993, Hopfield and Hertz 1995), which is consistent with experimental observations (Eckhorn et al. 1988, Neuenschwander and Singer 1996).

6. Phase coding – in this model times of emitted spikes are referred to the reference time point in a periodic signal. In this way neuronal spike trains can encode information in the phase of a pulse with respect to the background oscillations (Fig. 2F).

The concept of coding by phases has been studied both in models (Hopfield 1995, Maass 1996, Jensen Lisman 1996) and experimentally (Buzsaki 2006). Phase coding has been suggested for the hippocampus (O'Keefe 1993), the olfactory system (Laurent 1996), and also other areas of the brain, where oscillations of some global variable (for example the population activity) are quite common (Buzsaki 2006).

Spiking networks exploring the phase coding strategy have recently been used in such tasks as odor discrimination (Chen et al. 2011) or robot navigation (Kiss et al. 2006).

It is important to note that the experimental and theoretical findings discussed in this section do not discard rate-based neural codes. They rather highlight the importance of precise timing of spikes to the neural information transmission and provide strong motivation for investigating computational properties of the systems that compute with precisely timed spikes.

LEARNING

Synaptic plasticity refers to the ability of synaptic connections to change their strength, which is thought to be the basic mechanism underlying learning and memory in biological neural networks (Baudry 1998).

Various forms of synaptic plasticity co-exist. They differ mainly on a time scale: some processes, e.g. pulse paired facilitation, decay on the order of about 10–100 ms; other processes, such as long-term potentiation (LTP) or long-term depression (LTD), persist for hours, days, or longer (Lømo 1966, Magleby and Zengel 1976, Abbott and Nelson 2000, Citri and Malenka 2008). Plasticity processes differ also in the conditions required for the induction. Some depend only on the history of presynaptic stimulation, independently of the postsynaptic response. Other forms of plasticity depend on the coincidence of pre- and postsynaptic activity, on the temporal order of pre- and postsynaptic spikes and possibly on other factors, such as a concentration of specific chemicals (Citri and Malenka 2008).

In this section we discuss various models of learning for spiking neural networks that explore spike-timing based synaptic plasticity.

Unsupervised learning

In 1949 Donald Hebb addressed for the first time the question on how synapses should change their weights in order to store information (Hebb 1949). In mathematical terms his idea is usually expressed as: $\Delta w_{ji} \propto \nu_i \nu_j$, where Δw_{ji} refers to the change of the strength of the synaptic coupling w_{ji} between the presynaptic neuron i and the postsynaptic cell j; and ν_i, ν_j represent the activities of those neurons, respectively. According to the Hebb's formula the coupling w_{ji} is strengthened whenever neurons i and j are simultaneously active. This formula did not account for the synaptic depression. Only later experimental and theoretical work elaborated on the conditions under which the potentiation and depression could interact at a single synapse (Stent 1973, Sejnowski 1977, Sejnowski and Tesauro 1989).

By modifying synaptic strengths Hebbian processes lead to the reorganization of connections within a neural network and under certain conditions may result in the emergence of new functions, such as input clustering, pattern recognition, source separation, dimensionality reduction, formation of associative memories or formation of self-organizing maps (for a survey, we refer to Hinton and Sejnowski 1999). Development of such properties through Hebbian process is commonly referred to as unsupervised learning, since no direct goal and thus no correction is necessary here for developing a function within a network (Barlow 1989, Hertz et al. 1991, Hinton and Sejnowski 1999).

The terms ν_i, ν_j in the Hebb's formula have traditionally been interpreted as neural firing rates. Recent neurophysiological findings, however, suggest that the Hebbian plasticity may also be influenced by the timing of individual spikes (Markram et al. 1997). Moreover, evidence from hippocampal and neocortical pyramidal cells indicate that the order of pre- vs. postsynaptic spikes may induce different Hebbian processes. In one experiment the relative timing of the presynaptic spike arriving at the synapse and the postsynaptic action potential has been systematically varied (Markram et al. 1997, Bi and Poo 1998). It has been observed that the resulting change in the synaptic efficacy after several repetitions of the experiment was a function of the relative differences of the spike times. Generally, presynaptic spikes preceding postsynaptic spikes have been observed to induce potentia-

tion, while the reversed order of spikes induced synaptic depression. This phenomenon has been termed Spike-Timing-Dependent-Plasticity (STDP). In some synapses, a process complementary to STDP has been observed, i.e. the synapses were weakened if the presynaptic input arrived shortly before the postsynaptic spike and the potentiation occurred if the presynaptic spike followed the postsynaptic one. This process is known as anti-STDP (or anti-Hebbian plasticity).

Interesting enough, the dependence of synaptic plasticity on timing of spikes has been predicted theoretically (Gerstner et al. 1996). A general phenomenological model describing various forms of the spike-based synaptic plasticity has been proposed by Gerstner and Kistler (2002a). This model can be expressed as:

$$\frac{\mathrm{d}}{\mathrm{d}t} w_{ji}(t) = a_0 + a_1 S_i(t) + a_2 S_j(t) \\ + a_3 S_i(t) \overline{S_j}(t) + a_4 \overline{S_i}(t) S_j(t), \tag{3}$$

where $w_{ji}(t)$ is the efficacy of the synaptic coupling from neuron i to j; $S_i(t)$ and $S_j(t)$ are the pre- and postsynaptic spike trains, respectively; each spike train is defined as a sum of the Dirac impulses at the firing times t^f , that is $S(t)=\sum_f \delta(t-t^f)$; terms $\overline{S_i}(t)$ and $\overline{S_j}(t)$ are the low-pass filtered versions of $S_i(t)$ and $S_j(t)$, respectively; $a_0,...,a_4$ are the constant coefficients that control the rate of change in the synaptic efficacy.

In Equation 3 it is assumed that apart from the activity-independent weight decay (a_0) and the Hebbian terms ($a_3 S_i(t) \overline{S_j}(t)$, $a_4 \overline{S_i}(t) S_j(t)$), the synaptic changes can be triggered also by the individual spikes at the pre- or postsynaptic terminal even without additional action potentials on the opposite site, as illustrated in Fig. 3. Depending on the parameter choice Equation 3 can describe STDP, anti-STDP or other forms of synaptic plasticity.

STDP-like processes have assumed an important role in many applications of spiking neural networks. They are of a special interest in the context of unsupervised learning in such tasks as: cluster analysis (Natschlaeger and Ruf 1998b, Bohte et al. 2002b, Landis et al. 2010), pattern recognition (Hopfield 1995, Natschlaeger and Ruf 1998a), independent component analysis (Clopath 2008, Klampfl et al. 2009, Savin et al. 2010), formation of self-organizing maps (Ruf and Schmitt 1998, Choe and

Miikkulainen 2000, Sanchez-Montanes et al. 2002, Veredas et al. 2008) or formation of associative memories (Gerstner and van Hemmen 1992, Maass and Natschlaeger 1998, Sommer and Wennekers 2001, Zamani et al. 2010). We review specific applications of SNN controlled by the STDP rules in the last section of this paper.

Supervised learning

Supervised learning was proposed as a successful concept of information processing in artificial neural networks already in the early years of the theory of neural computation (Rosenblatt 1958, Widrow and Hoff 1960, Widrow 1962, Werbos 1974). Recently, there has been increasing body of evidence that instruction-based learning is also exploited by the brain (Knudsen 1994). The most documented evidence for this type of learning in the central nervous system comes from studies on the cerebellum and the cerebellar cortex, and thus refers mostly to motor control and motor learning (Thach 1996, Ito 2000a, Montgomery et al. 2002). In particular, supervised learning is believed to be utilized by the neural motor centers to form internal representations of the body and the environment (Kawato and Gomi 1992a,b, Shidara et al. 1993, Miall and Wolpert 1996, Wolpert et al. 1998) or for behavioral simulations and the encapsulation of learned skills (Doya 1999). Learning from instructions is supposed also to control information representation in sensory networks (Gaze et al. 1970, Udin 1985, Knudsen 1991). It is likely that supervised learning also contributes to the establishment of networks that support certain cognitive skills, such as pattern recognition or language acquisition, although there is no strong experimental confirmation of this proposition (Knudsen 1994, Thach 1996, Ito 2000b, 2008).

Instruction signals for supervised learning are thought to have a form of activity templates to be reproduced (Udin and Keating 1981, Miall and Wolpert 1996) or error signals to be minimized (Georgopoulos 1986, Kawato and Gomi 1992a, Montgomery et al. 2002). There is evidence that, in the nervous system, these signals are provided to learning modules by sensory feedback (Carey et al. 2005) or by other 'supervisory' neural structures in the brain (Doya 1999, Ito 2000a). But how are the instructions exploited by the learning neural circuits? What is the exact neural representation of the instructive signals? And, finally, how do biological neurons learn to generate desired outputs

given these instructions? Despite the extensive exploration of these topics the exact mechanisms of supervised learning in biological neurons remain unknown.

Whereas there is a well documented and richly represented group of supervised learning models for rate-based neurons (Kroese and van der Smagt 1996, Rojas 1996), spike-based coding schemes are still highly uncovered in this regard by the existing approaches. Only recently several concepts have been proposed to explain supervised learning in biologically realistic neuron models operating on the precise timing of particular action potentials (Kasinski and Ponulak 2006).

Supervised Hebbian Learning (SHL) offers probably the most straightforward solution for the implementation of supervision in a biologically realistic manner. According to this approach a spike-based Hebbian process (cf. Eq. 3) is supervised by an additional 'teaching' signal that reinforces the postsynaptic neuron to fire at the target times and to remain silent at other times. The 'teaching' signal is usually transmitted to the neuron in a form of synaptic currents or as intracellularly injected currents. A thorough analysis of the supervised Hebbian learning in the context of spiking neurons was performed by Legenstein and coworkers (2005). The authors demonstrated that the learning algorithm was able to approximate arbitrary mapping from input to output spike trains with satisfactory spike train precision. The authors
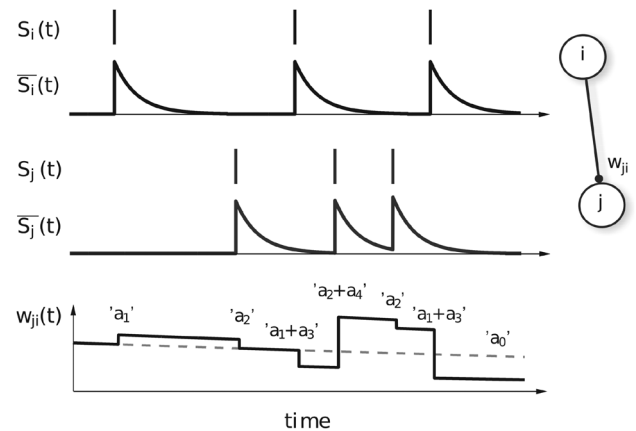

Fig. 3. Illustration of the spike timing dependent plasticity model given by Equation 3. From top to bottom: presynaptic spike train $S_i(t)$; synaptic trace $\overline{S}_i(t)$ of $S_i(t)$; postsynaptic spike train $S_j(t)$ and its synaptic trace $\overline{S}_j(t)$; changes of the synaptic weight $w_{ji}(t)$ induced by the particular terms in Equation 3 (referred to by coefficients given in quotes). Dashed gray line in the bottom plot illustrates the activity-independent weight decay (a_0).

reported, however, the following drawback of the algorithm: since teacher currents suppress all undesired firings during training, the only correlations of pre- and postsynaptic activities occur around the target firing times. At other times, there is no correlation and thus no mechanism to weaken these synaptic weights that lead the neuron to fire at undesired times during the testing stage. Another reported problem is that synapses continue to change their weights even if the neuron fires already exactly at the desired times. Thus, stable solutions in SHL can be achieved only by assuming some additional constraints or extra learning rules.

These problems are resolved in ReSuMe, another supervised learning algorithm introduced in Ponulak (2005). Similarly to SHL, the latter algorithm takes advantage of the Hebbian (correlation) processes, however, an instructive signal that modulates synaptic plasticity is supposed to have no- or only a marginal direct effect on the postsynaptic somatic membrane potential (Ponulak and Kasinski 2010). In ReSuMe, synaptic weight changes are modified according to the following equation:

$$\frac{\mathrm{d}}{\mathrm{d}t}w_{ji}(t) = a\left[S_d(t)\overline{S_i(t)} - S_j(t)\overline{S_i(t)}\right] = \\ = a\left[S_d(t) - S_j(t)\right]\overline{S_i}(t), \qquad (4)$$

where: a is the learning rate, $S_d(t)$ is the target (reference) spike train, $S_j(t)$ is the output spike train and $\overline{S_i}(t)$ is the low-pass filtered input spike train. We note that the middle part of Equation 4 describes ReSuMe as a method combining two Hebbian processes: the first one defined over the target and presynaptic spike trains, and the latter, anti-Hebbian one defined over the pre- and postsynaptic trains. The right hand side part of Equation 4 has a similar form to the Widrow-Hoff rule known from the theory of supervised learning in artificial non-spiking neural networks (Widrow and Hoff 1960). Indeed, ReSuMe can be considered as an extension of the Widrow-Hoff rule to spiking neural networks. We deliberately present here both equivalent forms of the ReSuMe algorithm to emphasize the role of the method in providing continuity between the well-established principles of supervised learning theory and the physiological mechanisms able to implement the learning algorithm in a biologically plausible way. For a detailed discussion on this topic we refer a reader to Ponulak and Kasinski (2010).

It has been demonstrated that ReSuMe enables effective learning of complex temporal and spatio-temporal spike patterns with high accuracy (cf. Fig. 4). The algorithm has also proven to be efficient in such computational tasks as: spike train prediction, forecasting, classification, pattern generation and motor control (Ponulak et al. 2006, 2008, Ponulak and Kasinski 2006b, 2010, Belter et al. 2008, Ponulak and Rotter 2008).

Whereas supervised Hebbian learning and ReSuMe are primarily suitable for training in single-layer networks[2], in many tasks it is more desirable to use multi-layer feedforward or recurrent neural networks. The reason is that the multi-layer and recurrent networks are typically capable of performing more complex computation than single-layer networks (Hertz et al. 1991). In the case of artificial non-spiking neural networks with continuous activation functions backpropagation algorithm has successfully been used to solve the problem of credit assignment in multi-layer networks (Werbos 1974, Rumelhart et al. 1986). However, implementation of error backpropagation in spiking networks is difficult due to the complex and, in many models, discontinuous dynamics of spiking neurons. In this case indirect approaches or special simplifications must be assumed in order to estimate gradient of the error.

One of the first algorithms to address this problem has been proposed by Bohte and colleagues (2000, 2002a). In their algorithm, known as SpikeProp, the authors implemented a gradient descent-based error backpropagation for multi-layer spiking neural networks. The major limitation of their method, however, was that each neuron was supposed to fire only once during a single simulation cycle and the time course of the neuron's membrane potential after the firing was not considered. The original SpikeProp algorithm has been thoroughly analyzed and various modifications have been proposed (Xin and Embrechts 2001, Moore 2002, Schrauwen and Campenhout 2004, Tino and Mills 2005). However, only several years later Booij and Nguyen (2005) and Ghosh-Dastidar and Adeli (2009) proposed two other algorithms derived from SpikeProp that would learn patterns composed of multiple spikes.

Interesting enough, many of the questions posed here, concerning supervised learning in spiking neu-

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[2] See, however, Ponulak and Rotter (2009) for application of ReSuMe to multi-layer networks.

ral networks, have also been asked in the context of the cerebellum, which is thought to be the primary site for supervised learning in the brain (Marr 1969, Albus 1971, Ito 2005, Jörntell and Hansel 2006). Accordingly, several spiking models of cerebellar supervised learning have been proposed (e.g. Yamazaki and Tanaka 2007, Achard and De Schutter 2008, De Schutter and Steuber 2009, De Sousa et al. 2009), along with some attempts to explain cerebellum-related aspects of motor adaptation (Medina and Mauk 1999, Hofstötter et al. 2002, Inagaki et al. 2007, Carrillo et al. 2008).

Up to now many other interesting algorithms for supervised learning in spiking networks have been proposed, including: Sougne (2001), Pfister and others (2006), Gütig and Sompolinsky (2006), Schrauwen and Campenhout (2006). For a review of some of those methods we refer to Kasinski and Ponulak (2006).

Reinforcement learning

Animals learn new behaviors not only through direct instructions, but more often by exploring available actions in the presence of reward signals. In a process of trials and errors desired actions are reinforced with positive rewards, whereas undesired actions are penalized by negative reward signals. Such a learning scenario has been termed reinforcement learning and has successfully been applied to the field of machine learning. However, a direct link between the theory of reinforcement learning and its biological neural implementation has for long been missing. Only recently, some progress has been made to connect theories of reinforcement learning to observed adaptation of neuronal processing. In particular, it has been observed that the activity of midbrain dopaminergic neurons is consistent with the reward signals predicted by the theory of reinforcement learning (Schultz 2002).
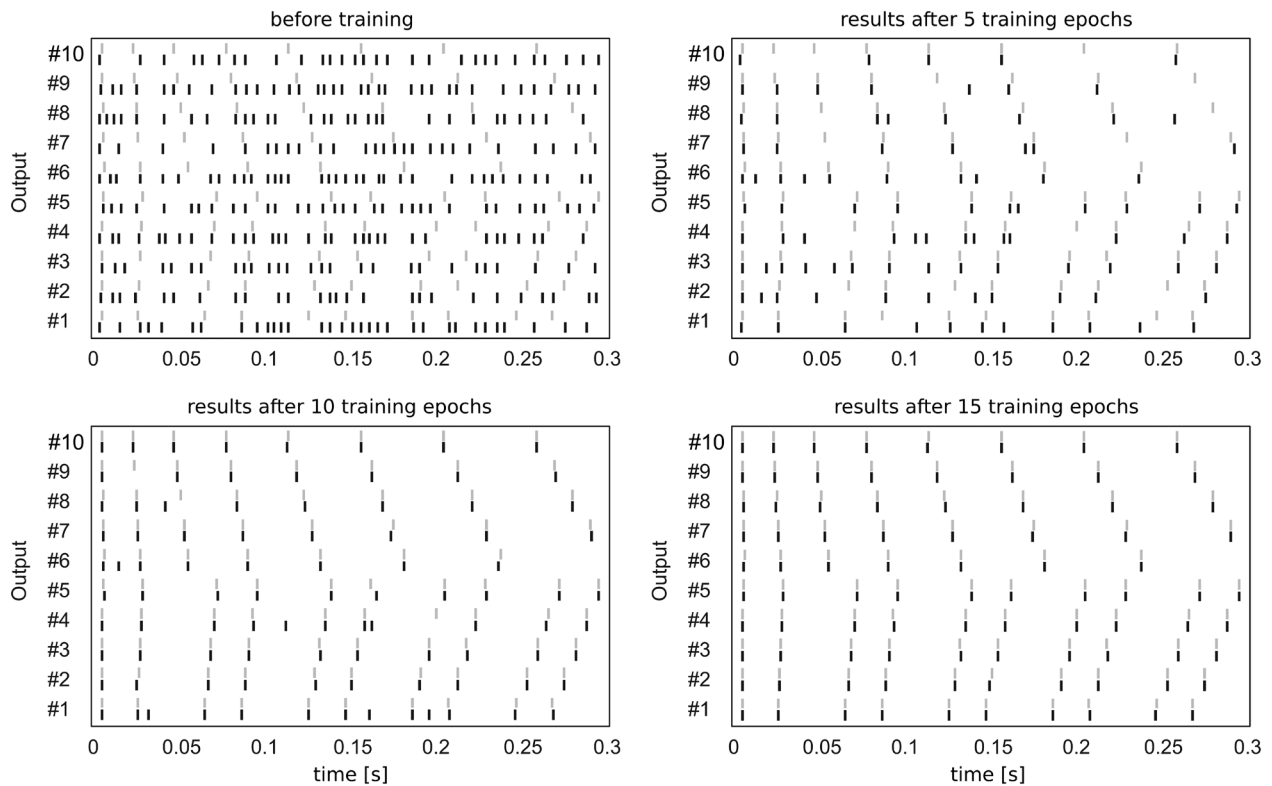

Fig. 4. Illustration of supervised learning with the ReSuMe algorithm. A single-layer feedforward network with 10 LIF neurons and 500 inputs is presented with a spatio-temporal spike pattern generated with a 5Hz Poissonian process. The task is to learn a sample target sequence of spikes assigned individually to each LIF neuron. The particular panels are the raster plots of the target firing times (gray vertical bars) and output firing times (black vertical bars) observed before- and after n training epochs, as indicated in the figure labels. Note, that already after 15 learning epochs all target patterns are almost perfectly reproduced at the network outputs.

It has also been shown that the concentration of dop-amine, a neuromodulator emitted by dopaminergic cells, controls plasticity processes in various brain areas (Otmakhova and Lisman 1996, Otani et al. 1998, Gurden et al. 2000, Bao et al. 2001, Lovinger 2010).

Based on these observations several models for rein-forcement learning in spiking neural networks have been proposed (Florian 2005, Baras and Meir 2007, Farries and Fairhall 2007, Florian 2007, Izhikevich 2007, Vasilaki et al. 2009). Many of these models can be expressed by the following general formula (cf. Legenstein et al. 2008):

$$\frac{\mathrm{d}}{\mathrm{d}t} w_{ji}(t) = c_{ji}(t) d(t), \tag{5}$$

where w_{ji} is, again, the weight of a synapse from neu-ron i to neuron j, $c_{ji}(t)$ is an eligibility trace of this synapse which collects weight changes proposed by STDP (cf. Eq. 3), and $d(t){=}h(t){-}h_o(t)$ corresponds to the concentration of the neuromodulatory signal $h(t)$ around its mean value $h_o(t)$. The learning rule given by Equation 5 is illustrated in Fig. 5. It is worth noting that this learning rule can be used to modify synaptic connections both within feedforward (Florian 2007) and recurrent spiking networks (Florian 2005, Legenstein et al. 2008, Vasilaki et al. 2009).
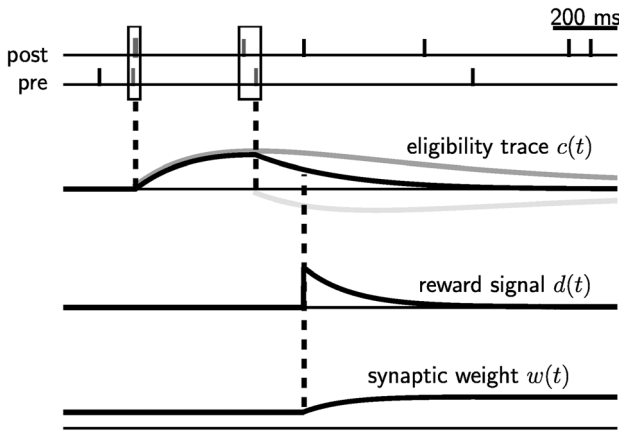

Fig. 5. Illustration of the spike-based reinforcement learning rule given by Equation 5 Here, changes of the synaptic weight w(t) are proportional to the product of the STDP eligibility trace c(t) with the reward signal d(t). Contribution of a pre-before-post spike pair and a post-before-pre spike pair to the eligibility trace c(t) is illustrated at the top of the figure (reproduced from Legenstein et al. 2009, with permission in accordance with the Creative Commons Attribution License).

The proposed models linking reinforcement theory and spike-based synaptic plasticity have been used to explain a number of experimentally observed phenom-ena, such as e.g.: shift of dopamine response from unconditional stimulus to reward-predicting condi-tional stimulus in classical conditioning (Ljungberg et al. 1992, Schultz 2002); learning the association of a stimulus with a proper response through instrumental conditioning (Thorndike 1901, Skinner 1953, Brembs et al. 2002); or direct control of a neural activity through biofeedback (Fetz and Baker 1973).

Spiking neural networks trained according to the reinforcement learning models have also been demon-strated to successfully solve many engineering tasks. This is the topics of the following section.

APPLICATIONS

In line with a structure of the previous section we present an overview of spiking neural network applica-tions categorized according to the used learning para-digms.

Many implementations of unsupervised learning in perceptron- or sigmoidal-gate-based ANN have been applied to real-world tasks. Recently, also SNN trained according to the Hebbian paradigm have been success-fully used in such tasks as: formation of the self-orga-nizing maps (Ruf and Schmitt 1998, Ruf 1998), tempo-ral sequence recognition based on the subspaces clus-tering (Natschlaeger and Ruf 1998a), formation of associative memories (Knoblauch 2003), or extraction of principal components from spike trains (Gerstner and Kistler 2002b). This list covers rather abstract applications. However, there is also a number of spe-cific, real-life tasks performed with use of self-orga-nizing SNN:

1. real-world data classification – classification capabilities of spiking networks trained according to unsupervised learning methods have been tested on the common benchmark datasets, such as, Iris, Wisconsin Breast Cancer or Statlog Landsat dataset (Newman et al. 1998, Bohte et al. 2002a, Belatreche et al. 2003). Various approaches to information encoding and network design have been used. For example, Bohte and coauthors (2002b) considered a 2-layer feedforward network for data clustering and classification. Based on the idea proposed in Hopfield (1995) the authors implemented models of local receptive fields combining the properties of radial

basis functions (RBF) and spiking neurons to convert input signals (classified data) having a floating-point representation into a spiking representation. The authors also proposed a spike-timing dependent Hebbian learning rule that enabled separation of complex clusters by synchronizing the neurons coding for parts of the same cluster. Classification results have been communicated in two ways: a neuron to fire communicated a classification decision (a winning cluster), whereas the firing time of this output neuron reflected the distance of the evaluated pattern to the cluster center. The approach proposed by Bohte and colleagues has been shown to outperform several other non-spiking classification methods when tested on the Fisher's Iris-dataset (Newman et al. 1998).

2. image recognition – using a feedforward network with the STDP-learning and the rank-order coding model, Thorpe and colleagues proposed a method for ultra-fast image categorization (Thorpe et al. 2001, Guyonneau et al. 2004, Perrinet et al. 2004). The network architecture developed by this group, consisted of two layers of neurons. At each step of categorization learning, one of the images to be classified was presented to the network. The presentation triggered a single spike in each neuron in the first network layer. Times of those spikes were then jittered and a Poisson-inspired spontaneous activity was added to the spike pattern at each presentation. The incoming activity was propagated towards the next layer. The first neuron to fire in the second layer inhibited its neighbors and triggered the STDP learning rule. As a result each neuron has learned one stimulus and one only. Similar learning principles have also been applied in algorithms for detection and classification of visual objects in complex intensity images (Guyonneau et al. 2004, Perrinet et al. 2004), or for image compression and reconstruction (e.g. Perrinet and Samuelides 2002). Several other models for unsupervised image recognition have been proposed (e.g. Muresan 2002, Kornprobst et al. 2005, Shin et al. 2010).

3. odor recognition – spiking models of the olfactory system have been proposed (e.g. Rochel et al. 2002, Brody and Hopfield 2003, Raman and Gutierrez-Osuna 2004, Finelli et al. 2008). In Martinez and Hugues (2004) a model of the insect locust antennal lobe has been implemented in SNN and used in a tracking experiment where a mobile robot was supposed to approach an odor source. In the proposed model, a stimulus was encoded by a spatial assembly of quasi-synchronized projection neurons, each one being individually phase-locked to local oscillations. A frequency adaptation has been used for temporal evolution of the spatial code aiming at enhancing the distance between the representations of similar odors.

4. spatial navigation and mental exploration of the environment – an interesting model of the hippocampus like network that can learn mental maps of the environment and which enables movement planning within a given environment has been presented in (Hopfield 2010). The network consists of a set of place cells with all-to-all excitatory connections. The particular place cells get activated as a simulated animal explores different locations in the environment. Spike-timing-dependent-potentiation is used to strengthen connections between cells activated in a close temporal proximity. Consequently, the cells that represent neighboring locations in the environment develop strong synaptic interactions. This mechanism is later used for path planning, where a localized bump of activity is initiated in the present animal's location and travels through the network along the neuronal pathways with the strongest connections until it reaches a selected target location. A simple motor control algorithm is proposed that uses the activity bump to guide the movement of the animal.

Not only Hebbian learning has proven to be useful in practical applications. Spiking networks trained according to the supervised paradigm have also been used in a number of tasks, such as:

• motor control and trajectory tracking – several models of spiking neurocontrollers have been proposed for the trajectory tracking and set point control tasks (Hofstötter et al. 2002, Joshi and Maass 2005, Burgsteiner 2005, Ponulak and Kasinski 2006b, Ponulak et al. 2006, Belter et al. 2008, Carrillo et al. 2008, Ponulak and Rotter 2008, Ponulak et al. 2008). For example, Joshi and Maass (2005) demonstrated that a liquid state machine network with a set of linear readouts could be trained to generate basic arm movements, both on a simplified 2 degree-of-freedom pendulum model, as well as on a biologically inspired arm model. After training the network could successfully generalize the acquired knowledge by generating movements to new end-points. Interestingly, the controller has been shown to be robust to feedback delay in a range similar to feedback latency observed in biological sensory-motor systems.

In Paolo (2003a,b) an evolutionary approach has been used to train a spiking controller in a mobile robot navigation task. The robot was supposed to perform positive phototaxis in the absence of sound stimuli and to perform negative phototaxis in the presence of a short-lived aversive sound stimulus. The search algorithm was able to find successful controller rules by evolving only the plasticity models and the time properties of each neuron. Both spiking and rate-based network models have been tested. It has been found that spiking controllers with STDP rules were able to reach a stable state more rapidly and more reliably than the rate-based counterparts under the same conditions, and achieved higher fitness by being able to accomplish the task earlier in their lifetimes.

• supervised data classification – spiking classifiers employing supervised learning paradigm have been used in several tasks that require classification of temporal signals, including classification of spike patterns (Maass et al. 2002a, Nikolic et al. 2009, Ponulak and Kasinski 2010), speech recognition (Hopfield and Brody 2000, 2001, Verstraeten et al. 2005, Gütig and Sompolinsky 2009) or epilepsy detection (Ghosh-Dastidar and Adeli 2009).

In Ponulak and Kasinski (2010) a liquid state network trained according to the ReSuMe algorithm has been used to classify categories of input signals encoded in temporal patterns of spikes. The network has been trained to communicate classification results by emitting precisely timed spike trains associated with the particular categories of input signals. It has been demonstrated that the network could perform correct classification even if stimuli were degraded by noise (jitter of spikes) and a decision time was delayed with respect to the stimulus presentation. Interesting enough, in the extreme case the classification was allowed to be made only 500 ms after the stimulus offset, based solely on the stimulus trace left in the firing activity of the recurrent circuit. Despite the fact that this trace would typically be overlapped by the ongoing network activity, the network was still able to classify input patterns with 70% of correct decisions.

A similar classification task, but with real spike patterns obtained from the multi-electrode recordings, has been considered by Nikolic and colleagues (2009). Here the authors analyzed neural activity of around 100 neurons in the cat primary visual cortex during the presentation of sequences of up to three different visual stimuli (letters of the alphabet). Using low-passed filtered versions of the recorded spike trains and a simple linear readout (a linear neuron) the authors demonstrated that it was possible to extract most of the information about visual stimuli extractable by sophisticated methods of machine learning, e.g. support vector machines with nonlinear kernel functions. Interesting enough, the results presented in the paper indicated that the network from which the recordings have been made shared similar properties to those postulated for reservoir computing concept.

One of the first spiking models of supervised speech recognition has been proposed in Hopfield and Brody (2000, 2001). In their model, the authors explored the phenomenon of transient synchronization of a group of neurons with convergent firing rates. Using this model, the authors tested the network for spoken digit recognition. It has been shown that the proposed network was able to perform broad generalization, even from a single example, and was robust to noise. Other interesting models for speech recognition have been proposed e.g. in Verstraeten and others (2005), Gütig and Sompolinsky (2009).

• decision making with application to financial market – a spiking neural architecture that combines supervised learning and fuzzy reasoning has been proposed as an expert system for evaluating financial fitness of companies operating within certain market sectors (Glackin et al. 2008).

Finally, spiking neural networks trained with reinforcement methods have been applied to such tasks as:

• spatial navigation and path planning – in Vasilaki and coauthors (2009) a simplified hippocampal model has been used to solve the Morris water maze task. The network model consisted of the place cells – encoding the simulated animal location; and the action cells – that controlled animal behavior. A reward-modulated spiking timing dependent plasticity rule has been used to alter synaptic connections between cells in order to learn the appropriate sensory-motor mapping allowing the animal to find the right way through the maze (Fig. 6).

A similar navigation task has been considered in (Lee and Kwon 2008), where the authors investigated a spiking network architecture for the simulated helicopter positioning based on visual clues. Again, a reward-based STDP rule has been proposed to learn the set of actions bringing the helicopter from any arbitrary position to the target position.

• decision making and action selection – in Soltani and Wang (2010) a reinforcement learning paradigm is proposed that explains electro-physiological and behavioral data in two-choice decision experiments in animals. The model network consists of three-layers of neurons. The first layer is a set of cue-selective neural populations, each one activated upon the presentation of a certain cue. The sensory cue-selective neurons provide, through synapses endowed with reward-dependent Hebbian plasticity, inputs to two neural populations in an intermediate layer. These two populations encode reward values of two choice alternatives (action values). Combination of cues is accomplished through convergence of cue-selective neurons onto action value-encoding neurons. The latter project to a decision making circuit consisting of two competing (through mutual inhibition) populations. Correct decisions are rewarded through the potentiation of plastic synaptic connections contributing to this decision.

• rehabilitation – an adaptive biventricular pacemaker with a spiking neural network coprocessor is investigated in (Rom 2007). The role of the spiking network is to perform dynamic optimization of the pacing intervals. The network has three functional layers. In the input layer, different subgroups of synapses are excited selectively according to the average heart rate and in each subgroup of synapses each synapse is excited with a fixed predefined increasing time delay measured from the synchronizing atrial event. The authors propose a reward-based Hebbian algorithm that is applied to the second layer of the network and aims at finding opti-
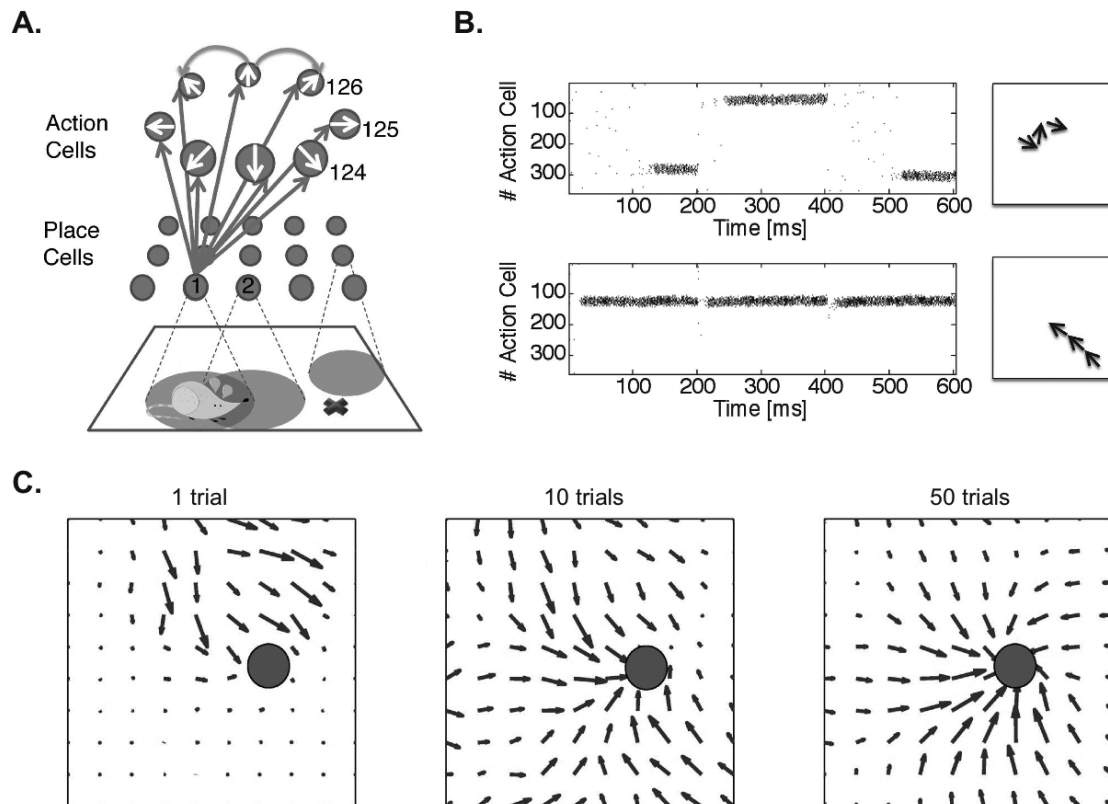

Fig. 6. Application of spiking neural networks to spatial navigation (Vasilaki et al. 2009). Here, a network trained according to the reinforcement learning paradigm has been used for animal navigation in a simulated Morris water maze experiment. (A) The network consists of two types of neurons: place cells – that are activated whenever an animal enters a certain spatial location; and action cells – that control animals behavior. Connections between place and action cells are altered by the learning process with the objective to find the correct action associated with every location of the animal, such that actions move the animal towards the target location. (B) Two sample sequences of the activity of action cells (left) and the corresponding animal behavior (right) are shown. (C) Navigation map of the animal visualized by a set of direction vectors. Plots from left to right show map formation after 1, 10 and 50 trials, respectively (modified from Vasilaki et al. 2009, with permission in accordance with Creative Commons Attribution License).

mal pacing intervals for a given heart condition. The last – output layer is composed of two sets of LIF neurons that accumulate postsynaptic responses from the middle layer and manage the pacing of the right and left ventricles. For security reason the SNN processor operates in a master-slave architecture that allows complete operation of predetermined boundaries set by a master controller. According to the authors of the paper, the proposed SNN-based system shows a 30% increase of performance in simulated cardiac output as compared to a nonadaptive biventricular pacemaker.

In addition to the typically engineering or AI applications of spiking neural networks discussed here, there are other fields that can benefit from the use of spiking networks. A particularly interesting and promising area is the modeling and analysis of biological neural structures. Deeper insight into neural circuitry, information processing and plasticity in the central nervous system is fundamental e.g. for understanding the relationship between the physio-anatomical disorders at the neural level and the resulting mental or physical dysfunctions of a subject. The list of recent applications of SNN in this area encompasses studies on almost all brain regions. For an excellent source of information on those models we refer readers to ModelDB – an online neural model database (Hines et al. 2004) (database available from: http://senselab.med.yale.edu/ModelDb).

In this section we presented selected application of spiking neural networks classified according to the three paradigms: unsupervised, supervised and reinforcement learning. Whereas in the discussed applications the networks have typically been trained according to single-type learning rules falling into one of those categories, there are obviously systems which may benefit from combining different learning paradigms within a single network. For example, unsupervised plasticity mechanisms, such as those discussed in Savin and coauthors (2010), can be used to improve input separation properties of the reservoir networks (cf. Section 'Spiking Models') and the supervised learning rules, like ReSuMe (Ponulak and Kasinski 2010), will be used for training the network outputs. Supervised learning can also be combined with reward-based learning. This technique is often used in neural implementations of the actor-critic model (Witten 1977, Sutton and Barto 2002), where supervised learning

is applied to function approximation in networks representing actor or critic modules (Tham 1995, Jaksa et al. 1999). Such an approach has been used so far in the non-spiking neural implementations, but in principles the same approach should be possible with spiking networks. Similarly, supervised and reinforcement learning can be used together in systems where both, error signals (for supervised learning) and evaluation signals (for reinforcement learning) are available from the environment to a learning system. Examples of (non-spiking) neural network models exploring the supervised-reinforcement learning concept are described in Rosenstein and Barto (2004) and Conn (2007).

As a concluding remark we would like to note that the list of spiking neural network applications presented in this section is neither exhaustive nor complete. Our intention was rather to provide a reader with examples of tasks where spiking networks have been successfully used to solve real-world problems (for other reviews on applications of SNN see Cios and Sala 2000, Gerstner and Kistler 2002b, Bohte and Kok 2005, Belatreche et al. 2006, Paugam-Moisy 2006).

SUMMARY

In this paper we surveyed selected concepts on information processing and learning in spiking neural networks. These concepts have proven to be computationally useful both as theoretical models as well as tools for practical applications. Theory of spiking neural networks can further gain both, from the new algorithms derived within a framework of machine learning, as well as from new discoveries in neurobiology. In particular, it is expected that the availability of more efficient learning methods for spiking networks will bring benefit to new areas of applications. Particularly promising are possible future biomedical applications of spiking neural networks in tasks involving interactions of human body with external devices, such as in brain-machine interface systems or in neural prostheses. Still, more work is needed to further explore necessary technology that would allow for efficient and safe use of spiking neural networks in these tasks.

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