

Decoding spatiotemporal spike sequences via the finite state automata dynamics of spiking neural networks

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New Journal of Physics **10** (2008) 015010 (16pp)

Received 30 June 2007

Published 31 January 2008

Online at <http://www.njp.org/>

doi:10.1088/1367-2630/10/1/015010

Abstract. Temporally complex stimuli are encoded into spatiotemporal spike sequences of neurons in many sensory areas. Here, we describe how downstream neurons with dendritic bistable plateau potentials can be connected to decode such spike sequences. Driven by feedforward inputs from the sensory neurons and controlled by feedforward inhibition and lateral excitation, the neurons transit between UP and DOWN states of the membrane potentials. The neurons spike only in the UP states. A decoding neuron spikes at the end of an input to signal the recognition of specific spike sequences. The transition dynamics is equivalent to that of a finite state automaton. A connection rule for the networks guarantees that any finite state automaton can be mapped into the transition dynamics, demonstrating the equivalence in computational power between the networks and finite state automata. The decoding mechanism is capable of recognizing an arbitrary number of spatiotemporal spike sequences, and is insensitive to the variations of the spike timings in the sequences.

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1. Introduction

Meanings of temporally complex stimuli such as speech are embedded in patterns over time. Sensory neurons in areas such as the primary auditory cortex [1, 2] and the retina [3, 4] detect stimulus features within short time windows, and spike reliably whenever their preferred features appear. Different features are preferred by different sensory neurons. A stimulus that varies over a time span much longer than the time windows of the features drives spatiotemporal sequential spikes in the sensory neurons. Thus, a population of sensory neurons encode complex temporal stimuli into spatiotemporal spike sequences [5]. How the brain's neural networks read out such codes is an important unsolved problem [6]–[14].

In this paper, we propose a decoding mechanism based on the spiking dynamics of biological neural networks. We note that spatiotemporal spike sequences are analogous to text strings: assigning a unique letter to each sensory neuron (or to each group of sensory neurons that detect the same feature) transforms the spike sequences into strings of these letters (figure 1). Decoding spatiotemporal spike sequences can thus be done similarly to recognizing written words. Finite state automata (FSA) are powerful mathematical models of machines that recognize a class of written words that belong to regular languages [15, 16]. We show that the spiking dynamics of networks of neurons with transient bistable dendritic plateau potentials, which produce UP and DOWN states of the membrane potentials, can behave like FSA for decoding spatiotemporal spike sequences. Transitions between the UP and DOWN states are controlled by feedforward excitations and inhibitions from the sensory neurons, as well as lateral excitations between the neurons in the networks. A general connection rule is shown to ensure the mapping of any finite state automaton to the transition dynamics of the network. Our networks have the same computational power as FSA, and can recognize spatiotemporal spike sequences as complex and general as all text strings recognizable by FSA.

Our mechanism is biologically realistic. Transient bistable dendritic plateau potentials are observed in cortical neurons [17, 18]; lateral excitation, feedforward excitation and feedforward inhibition are general features of cortical microcircuitry [19]. This is unlike previous studies on relating neural computations to FSA, which were mostly performed on artificial neural networks [20]. There are other biologically plausible mechanisms of recognizing temporal patterns, such as those based on tapped delay lines [8], synaptic depression [9], detection of

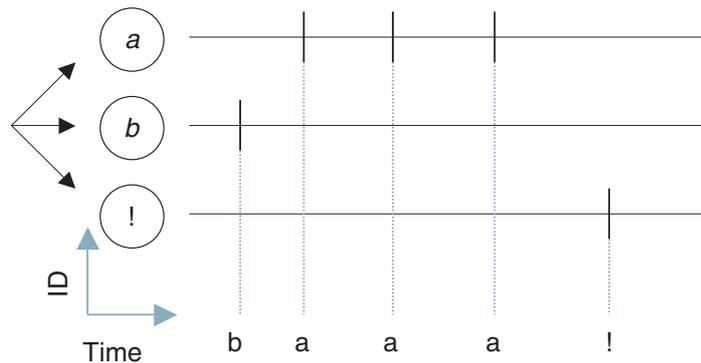


Figure 1. Transformation of spatiotemporal spike sequences into text strings. The sensory neurons are labeled with letters. Driven by time-dependent stimuli, the neurons spike at different times, indicated by the vertical bars. Such spatiotemporal spike sequences are analogous to text strings.

synchrony [10], transient network dynamics [11], or single neuron integration [13, 14]. Our mechanism is distinguished by its ability to process temporal patterns of arbitrary length, its tolerance of the timing variations of the input spikes, and its capability of recognizing, if necessary, an infinite number of patterns with common characteristics. It is an extension of our previous work on a similar mechanism that could recognize only a finite number of spatiotemporal spike sequences [12]. FSA is a key part of the Turing machine that is capable of universal computation [15], and also has been widely used in engineering systems such as natural language processing and speech recognition [16]. Our mechanism is a concrete demonstration that biological neural networks are computationally at least as powerful as FSA.

2. FSA

A FSA consists of a finite number of discrete states. Among them, one is designated as the start state, one or more as the end states and one as the ground state ϕ . Driven by sequential input letters from an alphabet, the FSA changes its states according to a transition table that decides the next state given the current state and input letter. A string of input letters may drive the FSA to one of the end states starting from the start state. If so, the string is said to be ‘recognized’ by the FSA. Otherwise, the string is said to be ‘rejected’. An example of a FSA that recognizes words in a ‘sheep language’ (strings starting with b , followed by one or more a ’s and ending with $!$) [16], is shown in figure 2. Consider a string $baaaa!$. At the beginning, the FSA is in S_1 , the start state; b induces a transition from S_1 to S_2 ; the first a from S_2 to S_3 ; subsequent a ’s from S_3 to S_3 and finally, $!$ from S_3 to S_4 ; since $!$ is at the end of the input and S_4 is an end state, the string is recognized. It is easy to see that the a ’s in between b and $!$ can be any number larger than zero, and all such ‘sheep words’ are recognized. Consider any string that starts with a . From S_1 , a induces a transition to the ground state ϕ , and the FSA stays in this state regardless of the subsequent inputs, thus S_4 is not reached at the end and the string is rejected. Similarly, a string like $bbaaa!$ is rejected because the FSA goes to ϕ after the second b . Incomplete sheep words such as $baaa$ are also rejected since at the end the state is S_3 not S_4 . The FSA rejects all strings that are not sheep words.

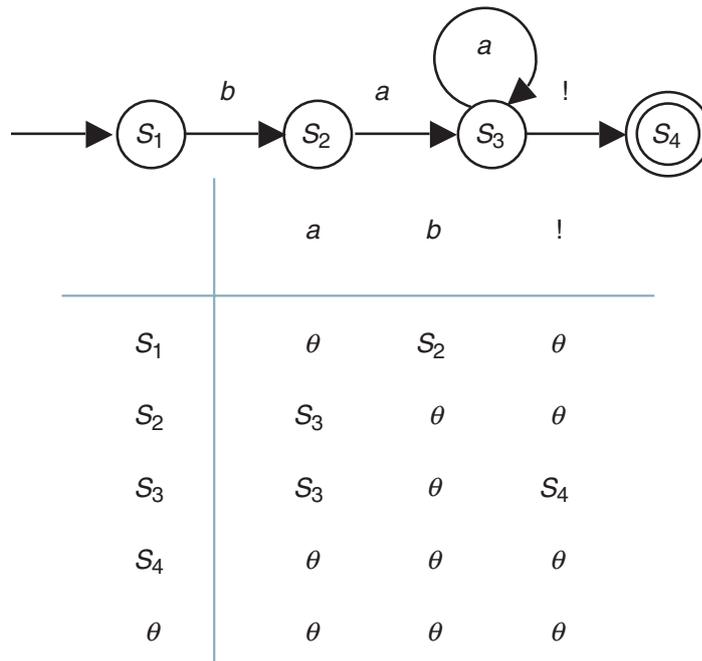


Figure 2. Finite state automaton that recognizes words in a ‘sheep language’ (strings of the form $ba \dots a!$). The automaton consists of five states. In the diagram, an arrow indicates transition from one state to the next upon receiving the input letter indicated near the arrow. The ground state ϕ and transitions to it are not shown. The start state S_1 is indicated with an incoming arrow with no source, and the end state S_4 is indicated with double circles. The complete transition rule is shown in the table. S_4 is reached if and only if the input string is a word in the sheep language, such as $baaa!$. The automata thus recognizes words in the sheep language, and rejects all other words such as $babba!aa$.

A key to the FSA computation is the AND operation. From a given state, the FSA can go to different states depending on the input. For instance, the sheep language automaton goes from S_3 to S_3 if the input is a , to S_4 if $!$ and to ϕ if b . Recognition of specific strings are through the transitions based on the state and input pairs. The ground state ϕ is a special state; once a FSA goes to that state, it remains there. Reaching the ground state at any point of an input signals rejection. The end state can be reached during an input; but if it is not reached at the end, the input is still rejected.

3. Neuron model

Experiments on excitatory neurons in the hippocampus [17] and the neocortex [18] demonstrate that a strong, excitatory, short (around 5 ms) pulse delivered at a distal branch of a dendrite can make the membrane potential of the branch go to a plateau potential that is transiently stable for 50–100 ms. This plateau potential then drives the membrane potential of the soma to a state that is depolarized about 10 mV above the resting potential of the neuron. We refer to this transiently sustained depolarized state as the UP state. Without the dendritic plateau

potential, the membrane potential stays near the resting potential. This is referred to as the DOWN state. A strong inhibitory input to the dendrite in the plateau potential can transit the UP state to the DOWN state. Our mechanism of decoding spatiotemporal spike sequences relies on these properties of cortical neurons. The idea is that the UP state corresponds to a state in FSA.

A common approach of modeling a neuron with dendritic structure is to approximate segments of the dendrites and soma as compartments that are connected according to the morphology of the neuron, each compartment described by its own membrane potential, ion channels and synaptic inputs. Such a model can be complex, with numerous compartments and detailed distributions of ion channels [21], if the aim is to accurately describe the morphological and biophysical properties of single neurons. Our goal here is different. We aim to show how dendritic plateau potentials can be utilized for decoding spike sequences with neural networks. We therefore choose to construct a simple multi-compartment model that incorporates only the neuron properties essential for our mechanism.

Our model of an excitatory neuron consists of a soma and five distal dendrites (the number of dendritic compartments is not critical). The dendrites are connected to the soma with ohmic conductance. The soma is a leaky integrate-and-fire unit: it generates a spike when its membrane potential exceeds a threshold. After the spike, the membrane potential resets to a reset potential, and remains there for a refractory period of 5 ms. The soma also contains A-type potassium conductance [22, 23], which is activated near the resting potential and inactivated at more depolarized potentials. This conductance enhances the robustness of our recognition mechanism. The dendrite is a leaky integrator as well, but does not generate spikes. All compartments have alpha-amino-3-hydroxy-5-methyl-4-isoxazolepropionic acid (AMPA) and gamma-amino-butyric-acid (GABA) synaptic conductances, which mediate synaptic excitation and inhibition, respectively. A dendritic compartment also has N-methyl-D-aspartate (NMDA) synaptic conductance (excitatory), whose nonlinear dependence on the dendritic membrane potential leads to a transient bistable plateau potential that drives the UP state of the soma [17]. The properties of the excitatory neuron model are shown in figure 3.

All synaptic conductances follow a ‘kick-and-decay’ dynamics. The decay time constants of AMPA and GABA conductances are 5 ms, while that of NMDA is 100 ms; the latter determines how long the UP state is sustained without further inputs. At the time of a spike arrival, the conductance of a synapse that receives the spike increases by an amount equal to the strength of the synapse. In between spikes, the synaptic conductance decays exponentially. Noisy fluctuations of the membrane potentials are induced by random excitatory and inhibitory spike inputs at the soma and the dendrites. Unless specified otherwise, we set the somatic and dendritic membrane potentials to fluctuate with 1 mV standard deviation. The mathematical details of the excitatory neuron model and the synaptic dynamics are given in the appendix.

We model an inhibitory neuron as a single compartment quadratic integrate-and-fire neuron [12, 24], on which the AMPA time constant is small (1 ms). It is capable of responding with a short latency to an excitatory spike input (figure 4(B)). The details of the model can be found in [12]. The AMPA conductance on the inhibitory neuron is set to 0.6; there is no NMDA conductance.

All synaptic and ion conductances are scaled with the leak conductances of the corresponding compartments.

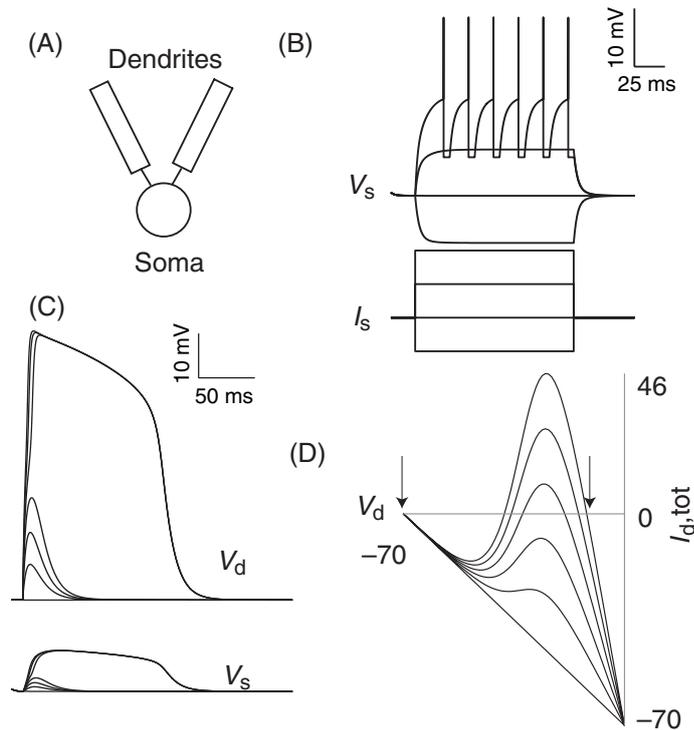


Figure 3. Properties of single excitatory neuron model. (A) The neuron consists of somatic and dendritic compartments. (B) Response profiles of the membrane potential V_s of the soma when injected with a constant current I_s in the soma at three levels. (C) UP and DOWN states of the membrane potentials. A brief excitatory input to a dendrite, when weak, leads to a brief and small depolarization of both the dendritic (V_d) and somatic (V_s) membrane potentials (DOWN state). When the input is strong, the membrane potentials sustain large depolarized plateau potentials (UP state). (D) The UP state is driven by a nonlinear current mediated through NMDA conductance in the dendrite. Several curves of the net current in the dendrite as a function of the membrane potential V_d , with different levels of NMDA conductances, are plotted. When the NMDA conductance is large, there are two stable equilibrium membrane potentials (arrows).

4. Network implementation of FSA

For any given FSA, we can wire the neurons in the following way to make the spiking dynamics of the network isomorphic to the FSA.

The number of states in the FSA equals the number of excitatory neurons. State S_i of the FSA is represented with neuron N_i in the UP state. The ground state ϕ corresponds to all neurons in the DOWN states.

For each letter in the alphabet of the FSA, there is one sensory neuron (or one group of sensory neurons) whose spikes indicate the detection of a distinctive feature (the neuron or the group is labeled with the letter). In addition, there is a ‘start neuron’ s that detects the beginning of a sensory input, and an ‘end neuron’ e that detects the end. A spike from a sensory neuron corresponds to a letter input to the FSA.

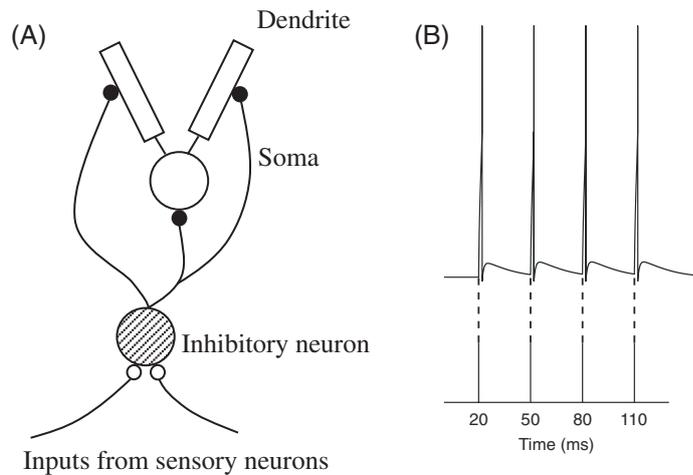


Figure 4. The connectivity and properties of the inhibitory neuron. (A) The inhibitory neuron (shaded) sends connections to the soma (synaptic strength G_5) and all dendrites (G_4) of every excitatory neuron. It receives inputs from all sensory neurons. (B) The inhibitory neuron spikes once with 2 ms delay to each spike input from the sensory neurons. The times of the input spikes are shown with vertical bars, and the membrane potential of the inhibitory neuron is plotted.

The state transitions are implemented through a network structure that agrees with observed microcircuitry of cortical neural networks [19]. All sensory neurons excite an inhibitory neuron, which in turn inhibits the somata (synaptic strength G_5) and dendrites (G_4) of all excitatory neurons (figure 4(A)). The inhibitory neuron spikes once with a delay of 2 ms at each input spike, thus providing a global feedforward inhibition to all dendrites and somata time-locked to each sensory spike (figure 4(B)). Sensory neurons also selectively send feedforward excitatory inputs to the somata (G_1) and the dendrites (G_2) (figure 5). Excitatory neurons selectively connect to the dendrites (G_3) to provide lateral excitation (figure 5). A dendrite is connected by at most one sensory neuron and one excitatory neuron. G_1 is in a range such that an input spike to the soma makes the neuron spike if it is in the UP state but not in the DOWN state; G_2 and G_3 are such that a dendrite cannot jump to the plateau potential if it receives only one spike from either a sensory neuron or an excitatory neuron, but can if it receives both; G_4 is large enough for a feedforward inhibitory spike to turn off the plateau potential at a dendrite in all cases except when the dendrite receives both feedforward and lateral spikes.

The AND operation $S_i \times h \rightarrow S_j$, which means transition from S_i to S_j if the input is h , is implemented by connecting sensory neuron h to the soma of neuron N_i , and both h and N_i to a dendrite of neuron N_j . There are no other excitatory connections to the dendrite. If N_i is in the UP state and h spikes, the dendrite goes to the plateau potential and makes N_j go to the UP state. Meanwhile, unless $i = j$, all dendrites of N_i are set to the resting potential due to the feedforward inhibition, and N_i returns to the DOWN state. This completes the operation.

At any moment, at most one neuron is in the UP state, and at most one dendrite of the neuron is in the plateau potential because different dendrites get inputs from different pairs of sensory and excitatory neurons.

The time intervals between input spikes are restricted to a range, since the transition between the UP and DOWN states takes a finite amount of time, and the UP state decays to

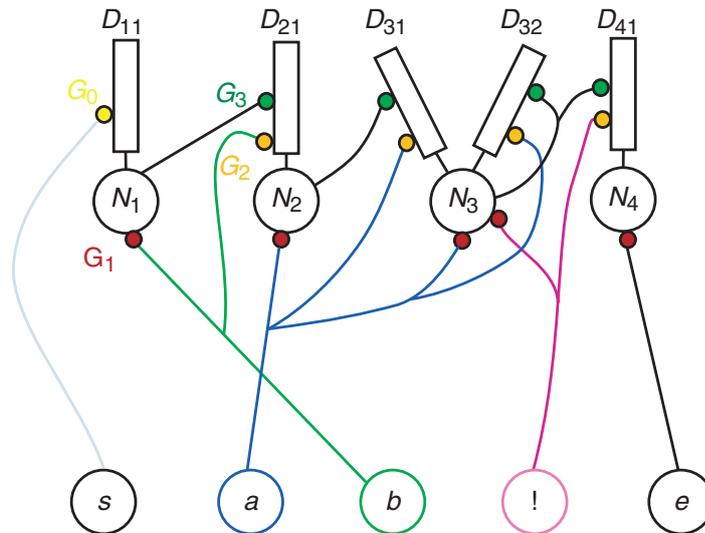


Figure 5. The network that decodes spatiotemporal spike sequences corresponding to the words in the sheep language. Sensory neurons, at the bottom, are labeled with their preferred features (s and e detect the start and end of the inputs). The inhibitory neuron and its connections are not shown. The somata and dendrites of the excitatory neurons are labeled with N and D , respectively. The dots at the end of the connection lines (axons) indicate synapses, red for the feedforward excitation to soma (synaptic strength G_1), orange for the feedforward excitation to dendrite (G_2), green for the lateral excitation to dendrite (G_3) and yellow for the input from the start neuron (G_0). Axons of sensory neurons a , b , $!$, s and e are indicated with blue, green, purple, gray and black, respectively. N_4 spikes at the end if and only if the sensory neurons spike in the sequence $sbaa \dots a!e$.

the DOWN state spontaneously if the interval is too long. We set the range from 30 to 80 ms. The start neuron s connects only to a dendrite of N_1 with synaptic strength G_0 (figure 5), which is strong enough to produce the plateau potential despite the feedforward inhibition. A spike from s makes N_1 go to the UP state, and the network is in the start state S_1 . The end neuron e connects to the somata of all neurons corresponding to the end states. When e spikes, one of these end state neurons spikes if it is in the UP state, indicating recognition of the input spike sequence. The recognition is signaled by the coincident spiking of e and an end state neuron. Spiking of the end state neurons before e spikes does not count.

The values of the synaptic strengths can be searched in the following way. Firstly, determine the range of G_1 by requiring that a feedforward input spike should not make the neuron spike in the DOWN state but should in the UP state. The A-current in the soma, which is inhibitory, is active in the DOWN state but inactive in the UP state; this makes the range of G_1 large. Secondly, determine the lower limit for G_4 . It must be large enough so that a spike from the inhibitory neuron can terminate the dendritic plateau potential and the UP state. Thirdly, for a value of G_4 beyond the lower limit, determine a range for G_2 and G_3 using two requirements: (1) they should be small enough so that a feedforward excitatory spike or a lateral spike alone cannot prevent the inhibitory spike from shutting down the plateau potential; (2) they should be

large enough so that a feedforward excitatory spike and a lateral excitatory spike together can produce the plateau potential from the resting potential despite the inhibition. Setting $G_2 = G_3$ simplifies the search process. Fourthly, G_0 is set to a large enough value to produce a plateau potential when s spikes. Finally, the role of the inhibition to the soma is to reduce the possibility that a neuron spikes during the transition from the DOWN to UP states due to the transient excitations at the dendrites, which can be large if G_2 and G_3 are large; G_5 is set accordingly. We have confirmed that there is a wide range of the parameters satisfying these criteria. For the rest of the paper, we set $G_1 = 2.5$, $G_2 = G_3 = 3$, $G_4 = 5$, $G_5 = 5$ and $G_0 = 5$.

5. The sheep language network

In figure 5, we show the network that implements the sheep language FSA (figure 2) and recognizes the spatiotemporal spike sequences that are analogous to the sheep words. There are four excitatory neurons, labeled N_1 to N_4 , whose UP states correspond to the states S_1 to S_4 . The network receives spike inputs from five sensory neurons, s , a , b , $!$ and e . One inhibitory neuron mediates global feedforward inhibition; it receives inputs from all sensory neurons and connects to all somata and dendrites of the neurons (not shown in the figure). s is connected to a dendrite D_{11} of N_1 ; this corresponds to the start arrow in the FSA transition diagram. b connects to the soma of N_1 and a dendrite D_{21} of N_2 , which also receives a connection from N_1 ; this implements $S_1 \times b \rightarrow S_2$. a connects to the soma of N_2 and a dendrite D_{31} of N_3 , which also gets a connection from N_2 ; this corresponds to $S_2 \times a \rightarrow S_3$. a also connects to the soma of N_3 and another dendrite D_{32} , which gets an autaptic connection from N_3 ; this implements $S_3 \times a \rightarrow S_3$. $!$ connects to the soma of N_3 and a dendrite D_{41} of N_4 , which is connected from N_3 ; this is $S_3 \times ! \rightarrow S_4$. Finally, e connects to the soma of N_4 , the end state neuron.

In figure 6(A), we illustrate the spiking dynamics of the network driven by input spike sequence $sbaaaa!e$, which is analogous to the word $baaaa!$ in the sheep language. The intervals between the input spikes are randomly chosen between 30 ms and 80 ms. The input sequence successively turns on the UP states in N_1 , N_2 , N_3 , N_3 , N_3 , N_3 and N_4 , and at the spike from e , N_4 spikes, indicating recognition of the input spike sequence.

From S_3 , the sheep language FSA stays in S_3 if the input is a , goes to S_4 if the input is $!$. In the network, the corresponding transitions are done through activations of different dendrites depending on the sources of the excitatory spikes. The soma of N_3 gets input from both a and $!$, thus can spike in the UP state if the input spike is from either a or $!$. However, a and $!$ connects to different dendrites: a to D_{32} of N_3 and $!$ to D_{41} of N_4 . D_{32} and D_{41} are also connected from N_3 . Thus, the input from a induces D_{32} to the plateau state and N_3 stays in the UP state, whereas the input from $!$ induces D_{41} to the plateau state and N_4 to the UP state. The dendrites hence implement the AND operations, and play a critical role in directing the network from the same state to different states with different inputs. It is easy to see that the network recognizes any input spike sequence of the form $sba \dots a!e$, which are analogous to the words in the sheep language.

The network rejects all spike sequences that are not analogous to the words in the sheep language. An example is shown in figure 6(B), in which the input sequence is $sba!bae$. The first three spikes $sba!$ of the sequence successively produce the UP states in N_1 , N_2 , N_3 and N_4 . However, the next input is from b , which does not send a connection to the soma of N_4 . At this input, none of the excitatory neurons spike and hence none of the dendrites get a lateral excitation; N_4 returns to the DOWN state due to the feedforward inhibition, and the network

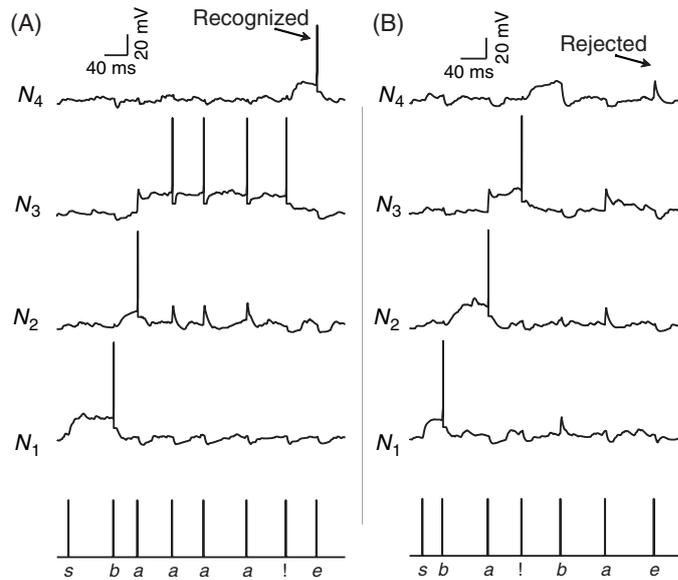


Figure 6. Somatic membrane potentials of the excitatory neurons in the network shown in figure 4, driven by input spike sequence (A) *sbaaaa!e* and (B) *sba!bae*. The lines at the bottom mark spike timings of the sensory neurons. In (A), N_4 spikes when e spikes, indicating recognition of the input spike sequence; in (B), it does not, indicating rejection.

goes to the ground state. Subsequent spike inputs cannot make any of the neurons go to the UP state, and the network remains silent. In particular, the spike from e does not make N_4 spike. The input sequence *sba!bae* is thus rejected. Similar reasoning shows that all non-sheep-language sequences, such as *sbbbaaba!!e*, are rejected. Hence, the spiking dynamics of the network shown in figure 5 is isomorphic to the FSA shown in figure 2.

6. Parity checking network

Even with a small number of neurons, our network can detect spike sequences with nontrivial characteristics. Consider a case of spike sequences from two sensory neurons a and b . The task is to recognize all sequences that contain odd numbers of spikes from both a and b , and reject all others. Two spike sequences can differ by only one spike, for instance *sbabbe* and *sbabbae*; yet one should be recognized and the other rejected. The order of the spikes does not matter.

For text strings, this parity-checking task can be solved with a FSA with four states, as shown in figure 7(A). The start state S_1 goes to S_2 with input b , to S_4 with a ; S_2 goes to S_1 with b , to S_3 with a ; S_3 goes to S_2 with a , to S_4 with b and S_4 goes to S_3 with b , to S_1 with a . From the state transition diagram it is easy to deduce that the end state S_3 is reached at the end only if the input string contains odd numbers of a and b .

The corresponding network is shown in figure 7(B), which is wired by implementing the FSA following the rule described previously. In figure 8(A), we show the dynamics of the network with input *sbbbbaaaabbabbaae*, which contains 7 a 's and 9 b 's. N_3 spikes when

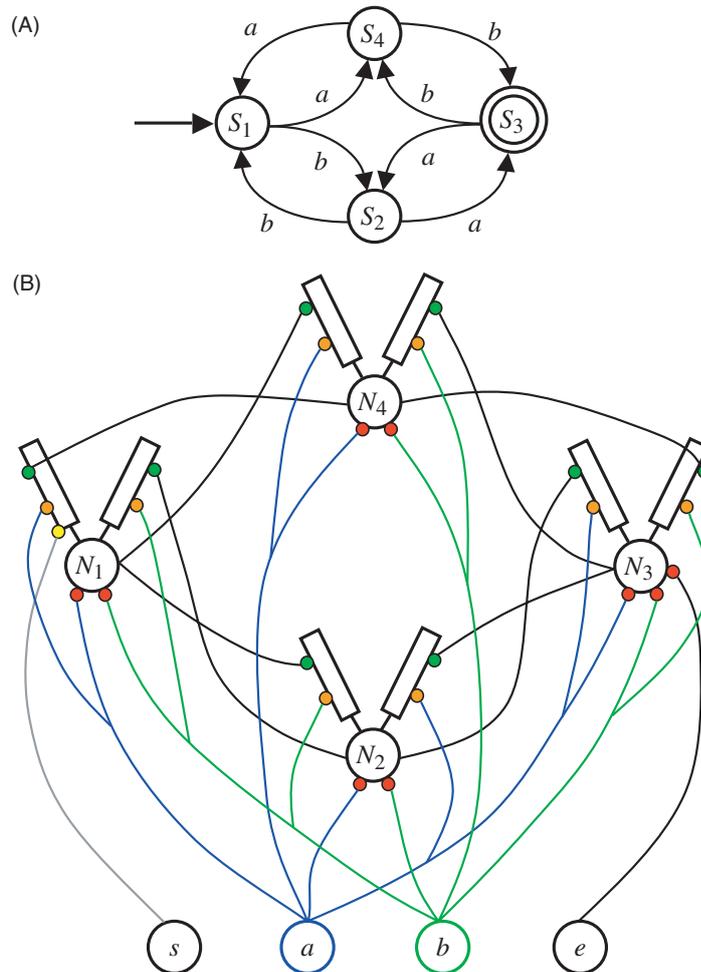


Figure 7. A finite state automaton that checks the parity of input strings consisting of a and b . (A) The state transition diagram. The end state S_3 is reached at the end of the input if and only if the input string contains odd numbers of a and b , for example, $aababb$. (B) The network corresponding to the automaton in (A). The convention is the same as in figure 5.

e does, indicating the recognition of the sequence. In figure 8(B), we show the case with input $sababaaaabbbaabbe$, which contains 8 a 's and 7 b 's. N_3 does not spike when e does, indicating the rejection.

The network can tolerate noisy fluctuations in the membrane potentials of the neurons to some extent. To show this, we vary the maximum strengths $G_{\text{soma,noise}}$ and $G_{\text{dendrite,noise}}$ of the random noise spikes, while keeping the standard deviations of the fluctuations in the soma and dendrites the same. For each noise level, defined as the standard deviation of the somatic membrane potential during a period of no sensory inputs, we generate 500 random spike sequences of a and b . The sequences are uniformly sampled from all possible ones containing 1–10 spikes of a and b . The intervals between the spikes are randomly selected from 30 to 80 ms, as before. We compute the percentage of recognitions of the sequences that should be recognized, and the percentage of rejections of the sequences that should be rejected. The results

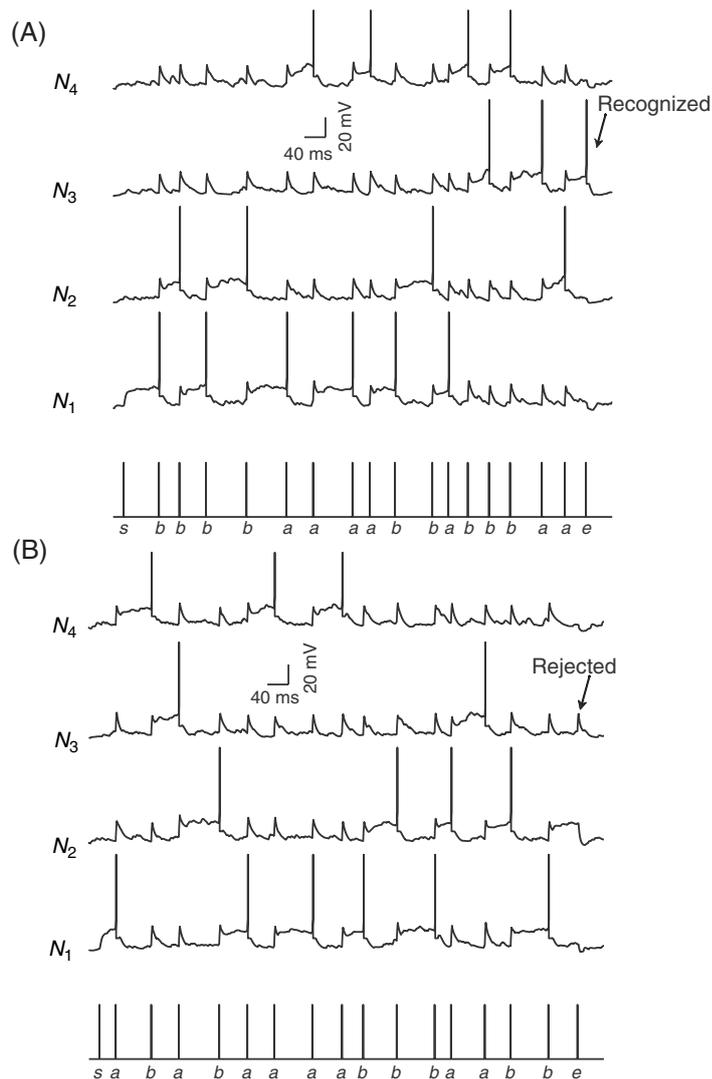


Figure 8. Somatic membrane potentials of the excitatory neurons in the network shown in figure 7(B), driven by input spike sequence (A) $s b b b b a a a b b a b b b a a e$, which contains 7 a 's and 9 b 's and (B) $s a b a b a a a a b b b a a b b e$, containing 8 a 's and 7 b 's. The lines at the bottom mark spike timings of the sensory neurons. In (A), N_3 spikes when e spikes, indicating recognition of the input spike sequence; in (B), it does not, indicating rejection.

are shown in figure 9. The network performance is perfect up to a noise level about 1 mV. Beyond this level, the rate of false positive (recognizing a sequence that should be rejected) and the rate of false negative (rejecting that should be recognized) go up. The rate of false positive tends to grow faster with the noise compared to the rate of false negative. This reflects the fact that with large noise, neurons tend to spend more time in the UP states, and the end state neuron spikes readily when e does.

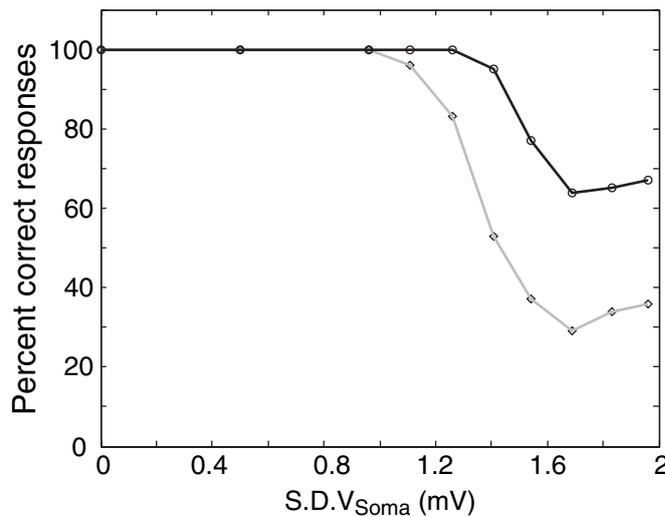


Figure 9. Performance of the parity checking network shown in figure 7(B) as a function of the noise level, defined as the mean of the standard deviations of the somatic membrane potentials of the excitatory neurons when there are no sensory inputs. The black line indicates the percentage of correct responses to the spike sequences that should be recognized, and the grey line is for the sequences that should be rejected.

7. Discussion

We have shown that biologically realistic neural networks can behave like FSA to decode spatial temporal spike sequences. The states of the networks consist of the UP states of neurons sustained by plateau potentials in the dendrites. The transitions between the states are controlled by feedforward excitation, lateral excitation and feedback inhibition. Coincident inputs of feedforward and lateral excitations are required for producing plateau potentials at the dendrites. This corresponds to the AND operation in FSA. Any FSA can be mapped into an equivalent network. Thus, the ability of our networks in recognizing spatiotemporal spike sequences is the same as that of FSA in recognizing text strings. One network can recognize an unlimited number of sequences with common characteristics, as demonstrated by the sheep language network and the parity checking network. The intervals between the spikes in the sequences can vary within a large range. Thus, the networks can handle uneven temporal warping of sensory inputs.

Our mechanism relies on transitions between network states for temporal integration. This is similar to previous proposals that used short-term synaptic depression [9] or transient network dynamics [11] for imprinting the temporal information of inputs to the network states. Unlike these proposals, however, our mechanism is capable of integration over arbitrarily long time, since the dynamics of our networks is stable due to the binary nature of the plateau potentials and the tight inhibitory control of the transitions. In principle, any network dynamics might be related to FSA; however, such a relationship is often at best speculative or implicit. Our mechanism is explicitly understood in terms of FSA.

We have used a single neuron to represent one state. A simple extension is to replace each neuron with a group of neurons. In this case, state transitions are accompanied by synchronous spiking of the neurons representing the same states. Since the role of individual neurons is

reduced, the networks should be more resistant to noise in single neurons. The same can be done with the inhibitory neuron. With a group of inhibitory neurons, the feedforward inhibition is accomplished by their synchronous spikes at each sensory input; random spiking of an inhibitory neuron does not matter. Replacing each sensory neuron with a group likewise should increase the robustness of the sensory inputs against noise.

Transitions between bistable membrane potentials are widely observed in cortical pyramidal neurons *in vivo* [25]–[27]. We propose that such state transitions in single neurons can be utilized to integrate temporal information. In our networks, spikes of the excitatory neurons occur near the UP to DOWN state transitions, although they can also be absent during the transitions. Whether this is true in the cortical neurons remains to be seen. This prediction should be modified if a state is represented with a group of neurons rather than a single neuron, which might be more realistic. In this case, the neurons representing the same state should spike synchronously during the UP to DOWN state transitions; random spiking of the neurons in the UP states can be allowed.

The beginning and end of a sensory input are signaled with the start and end sensory neurons, respectively. These boundary detecting neurons are similar to the ON and OFF neurons found in sensory areas such as the retina [4, 28] and the auditory cortex [29, 30]. In our sequence detecting networks, the neurons corresponding to the start and end states in FSA are connected by the start and end sensory neurons, respectively, and these specific connections are the only characteristic that distinguishes the start and end state neurons from others in the networks. The coincident spiking of the end sensory neurons and the end state neurons signals the recognition of a input spike sequence. The neurons in the networks have a wide range of input selectivity: while a start state neuron spikes whenever there is a sensory input, an end state neuron usually spikes only to highly complex input patterns. Other neurons have intermediate selectivity.

Our model of the excitatory neuron is quite simple, and only crudely approximates the complex dendritic structures of cortical neurons. Moreover, the model lacks the wealth of ionic conductances found in the dendrite and soma of cortical neurons, as well as neurotransmitters that can help to stabilize the UP states [26]. A more elaborate neuron model might improve the robustness of our networks against noisy fluctuations.

In our networks, the interneuron has highly convergent inputs and highly divergent outputs. It spikes reliably with a short latency to the inputs from the sensory neurons. Inhibitory neurons with these properties have been found in the somatosensory cortex [31]. Although we rely on feedforward inhibition for controlling the state transitions, it is possible to also include feedback inhibition, often found in cortical microcircuitry, as done in our previous work [12]. This should widen the range of the synaptic strengths that make the networks function properly [12].

An unresolved issue is how the specific connections between the excitatory neurons and those from the sensory neurons to the dendrites of the excitatory neurons might be set through experience. In computer science, learning FSA through examples is an active research area [32]. Such research might inspire biologically plausible mechanisms of learning the specific connectivity for recognizing a given set of spatiotemporal spike sequences.

Acknowledgments

This work was supported by an Alfred P Sloan Research Fellowship and The Huck Institute of Life Sciences at The Pennsylvania State University.

Appendix

The mathematical details of the excitatory neuron model are as follows. The dynamics of the membrane potential V_s of the soma is

$$\tau_s \frac{dV_s}{dt} = E_r - V_s + g_{ds} \sum_{j=1}^N (V_{dj} - V_s) + I_s + I_A + I_{\text{ext}},$$

and that for the j th dendrite V_{dj} ($j = 1-5$) is

$$\tau_d \frac{dV_{dj}}{dt} = E_r - V_{dj} + g_{sd}(V_s - V_{dj}) + I_{dj}.$$

Here, $\tau_s = 20$ ms and $\tau_d = 10$ ms are the membrane time constants of the soma and the dendrites, respectively; $E_r = -70$ mV is the resting membrane potential; $g_{ds} = 1.0$ is the conductance from dendrite to soma and $g_{sd} = 0.05$ is that from soma to dendrite. Note that the unit of all conductances on the soma is the somatic leak conductance, and that of those on the dendrite is the dendritic leak conductance. The synaptic current on the soma is given by

$$I_s = -g_{As}(t)V_s - g_{Gs}(t)(V_s - E_l),$$

where g_{As} and g_{Gs} are the AMPA and GABA conductances, and $E_l = -75$ mV is the reversal potential of inhibitory synapses (the reversal potential of excitatory synapses is 0 mV). The A-type potassium current in the soma is given by

$$I_A = -g_A a_{\infty}(V_s)^3 b(t)(V_s - E_K),$$

where $g_A = 10$ is the conductance; $E_K = -90$ is the reversal potential of potassium current; the activation variable a_{∞} is given by

$$a_{\infty}(V_s) = \frac{1}{1 + \exp(-(V_s + 70)/5)}$$

and the inactivation variable b is determined by

$$\tau_A \frac{db}{dt} = -b + \frac{1}{1 + \exp((V + 80)/6)},$$

with $\tau_A = 5$ ms. The kinetics of the A-current is modified from Shriki *et al* [23]. I_{ext} is an external current injected to the soma, and is set to zero except in figure 3(B) to show the soma property.

The synaptic current on the dendrite is given by

$$I_{dj} = -g_{Adj}(t)V_{dj} - g_{Gdj}(V_{dj} - E_l) - \frac{g_{Ndj}(t)V_{dj}}{1 + \exp(-(V_{dj} + 30)/5)}.$$

Here, besides the AMPA and GABA conductances g_{Adj} and g_{Gdj} , there is also a NMDA conductance g_{Ndj} through which flows nonlinear excitatory current responsible for the transient bistable plateau potential, as shown in figure 3(D).

In between spikes, all synaptic conductances decay exponentially. The decay time constants for AMPA and GABA conductance are both 5 ms, that for NMDA conductance is 100 ms. A spike arriving at an excitatory synapse with strength G on the soma leads to $g_{As} \rightarrow g_{As} + G$, and that to an inhibitory synapse leads to $g_{Gs} \rightarrow g_{Gs} + G$. On the j th dendrite, a spike to an excitatory synapse leads to $g_{Adj} \rightarrow g_{Adj} + G$ and $g_{Ndj} \rightarrow g_{Ndj} + \alpha G$, where $\alpha = 5.0$ is the ratio of NMDA and AMPA conductances on the dendrite. There is a saturation of the NMDA conductance; g_{Ndj} is not allowed to go beyond 10.0.

The soma generates a spike if $V_s > V_{th} = -54$ mV, and resets V_s to the reset potential $V_r = -64$ mV, and keeps $V_s = V_r$ for a refractory period of 5 ms. The dendrite does not generate spikes. Noisy fluctuations of the membrane potentials are induced by random excitatory and inhibitory spike inputs at the soma and the dendrites. In each compartment, the random excitatory spike times are generated according to a Poisson process with a rate of 200 Hz; the same for the random inhibitory spikes. The synaptic strength at each random excitatory or inhibitory spike is randomly selected from 0 to $G_{\text{soma,noise}}$ in the soma and 0 to $G_{\text{dendrite,noise}}$ in the dendrite. Unless specified otherwise, we set $G_{\text{soma,noise}} = 0.3$ and $G_{\text{dendrite,noise}} = 0.07$, which makes the somatic and dendritic membrane potentials fluctuate with 1 mV standard deviation.

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