

A Spiking Neural Model for the Spatial Coding of Cognitive Response Sequences

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Abstract— The generation of sequential responses is a fundamental aspect of cognitive function, encompassing processes such as motor control, linguistic expression, memory recall and thought itself. There is considerable evidence that complex cognitive responses (such as voluntary actions) are constructed as chunked sequences of more elementary response primitives or synergies, which can themselves be seen often as sequences of simpler primitives. Almost all neural models of sequence representation are based on the principle of recurrence, where each successive item is generated by preceding items. However, it is also interesting to consider the possibility of purely spatial neural representations that result in sequential readout of pre-existing response elements. Such representations offer several potential benefits, including parsimony, efficiency, flexibility and generalization. In particular, they can allow response sequences to be stored in memory as chunks encoded by fixed point attractors. In this paper, we present a simple spiking neuron model for the flexible encoding and replay of response sequences through the impulsive triggering of coding patterns represented as fixed point attractors. While not intended as a detailed description of a specific brain region, the model seeks to capture fundamental control mechanisms that may apply in many parts of the nervous system.

Index Terms—Cognitive control, sequence learning, spiking neural networks, attractor networks.

I. INTRODUCTION

A Developmental, dynamical and embodied view of cognition [1]-[15] inevitably requires mechanisms by which cognitive systems can “bootstrap” from simple behaviors to more complex ones over the course of development. These behaviors include not only external ones, i.e., actions, but also internal ones, such as recognition of objects, memory recall, decision-making, ideation, etc. All of these ultimately correspond to temporally evolving, synergistic patterns of activity across interacting complex

networks in the brain-body system comprising neural and musculoskeletal elements [1]-[15]. A useful way to think of cognitive systems is thus as generators of response sequences at multiple spatial and temporal scales, with more complex responses – both internal and external – constructed from the combination of simpler ones through development and learning. These combinations can be superpositional or sequential. For example, complex voluntary actions over extended periods can be seen as sequences of simpler actions, each of which may, in turn, be generated by a superposition of scaled and time-shifted stereotypical patterns of coordinated muscle activities called *synergies* [16]-[24]. Though these synergies combine through superposition, sequential combination remains extremely important since the basic synergy patterns are of short durations (at most a few hundred milliseconds), whereas actions (or other cognitive responses) can unfold over much longer periods. In some situations, the sequentiality becomes explicit, as in playing a musical instrument, learning a list of words, or composing sentences. The characteristics of such sequential learning and recall have been studied extensively through experiments in both monkeys and humans [25]-[28]. Several neurocomputational models of sequential processing have also been developed [29]-[31], but the focus in most of these models has been on learning and recalling specific sequences through explicitly temporal associations. In this paper, we describe a simple but flexible model for encapsulating sequences efficiently as spatial activity patterns, which is potentially extremely useful for building complex sequential responses from simpler ones through developmental learning.

II. BACKGROUND AND MOTIVATION

Almost all neural models of sequence representation have used a “chaining” approach, where successive items in the sequence are generated by association with previous items. However, it is interesting to consider whether response sequences can be represented by purely spatial patterns, and read out as sequences when needed. This is the essence of the competitive queuing (CQ) model proposed by Grossberg [32] to explain the phenomena of primacy and recency in the free recall of lists from working memory, and more recently by Grossberg and Pearson [33] as the basis of the LISTPARSE model. Experiments by Averbeck et al [34] have provided intriguing evidence that extended action sequences such as those involved in drawing or writing may be encoded initially

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as specific spatial patterns of activity, and then read out through an execution mechanism. However, the significance of this mechanism extends beyond its possible use in motor control. Since all cognitive function involves sequences of preconfigured response primitives – words, phrases, concepts, thoughts, memories, ideas, movements, muscle synergies, etc., the flexible and efficient representation of such sequences must be a fundamental function of the nervous system – in particular, the cerebral cortex. The explicit encoding of sequences in memory through associative chaining is very expensive and rather cumbersome, since each element of the sequence and every association between elements must be represented explicitly. In contrast, spatial patterns of activity can easily be learned as fixed point attractors in recurrent networks [35], and are extremely convenient as distributed neural representations. When the responses needed are *stereotypical* sequences of *preconfigured* response elements such as muscle synergies [16]–[24] or chunks [36]–[38], spatial representations are especially useful. Such responses occur, for example, in drawing and writing, playing familiar pieces of music, speaking familiar phrases, and in a vast array of other responses. They may also be important for the representation of temporal structure in semantic constructs, which is a poorly understood issue in cognitive neuroscience.

In this paper, we present a CQ-type model that allows the coding of responses sequences with specific temporal profiles, and show how this model allows representations that are both general and flexible. This approach offers several advantages:

- Representing sequences as spatial patterns makes them much simpler to store, recall and use.
- Spatial representations are more efficient than explicitly sequential ones because several items are represented in a single pattern.
- Multiple sequences involving the same items can be obtained from the same basic pattern simply by varying the modulation pattern. This *content invariance* can be the basis of both generalization and innovation. For example, once a certain pattern of movements has been learned, it can be reproduced easily with variable timing and novel permutations of it can be explored easily to discover other useful sequences.
- The model dissociates the timing of the sequence from its contents, allowing each to be learned separately. Thus, a relatively small number of canonical item patterns and modulation patterns can combinatorially and *systematically* produce a rich array of responses.
- The duration and rhythm of sequences can be varied very easily and flexibly by simply varying the modulation pattern *spatially*. In contrast, learning the same sequence with different timings in a chaining system is much more difficult and is more limited by the capacity of the system.

- The chunked patterns allow sequential structures to be loaded and used as single entities in working memory, and possibly in other systems [33].
- This scheme can be applied hierarchically to produce sequences at various spatiotemporal levels, greatly amplifying the richness of the system.

The model can be seen as a highly simplified version of the LIST PARSE model recently proposed by Grossberg and Pearson [33]. While that model is able to explain many specific phenomena observed in memory recall (e.g., bowed gradients of errors), its comprehensive scope makes it rather complex. Our model focuses more on the purely computational issue of flexibly representing complex sequential responses as spatial patterns in networks of spiking neurons, and the manipulation of these representations to generate variants. An important difference between our model and earlier CQ models is that here, the inactivation of a response element depends on a modulating input rather than purely on recurrent self-inhibition, as in LIST PARSE [33]. This makes the system computationally more flexible.

III. MODEL DESCRIPTION

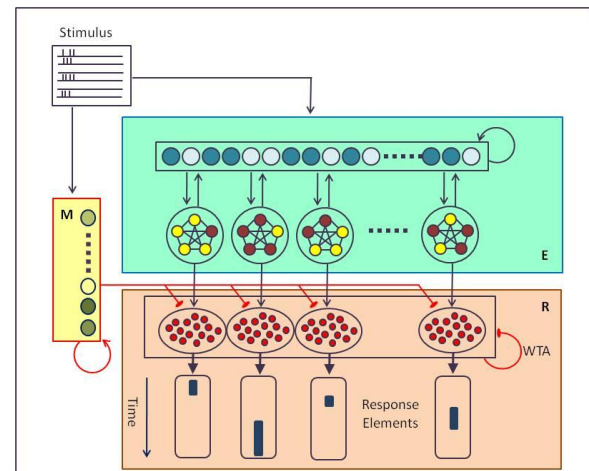


Figure 1: Architecture of the model showing the E, M and R systems. See text for details.

Overall Architecture

The architecture of our model is shown in Figure 1. The system comprises the following three subsystems:

The Encoding System (E): This system encodes response sequences as patterns of activity across a two-layer recurrent network. Each sequence is represented as an attractor pattern embedded in the network through Hebbian learning as described in the next section. Layer 1 of E receives a brief impulse stimulus, which triggers a specific attractor pattern across both layers. Neurons in Layer 2 project to the Response System, determining the composition and order of the response sequence generated.

The Modulation System (M): This system provides signals that determine the inactivation rate of neurons in the Response System, R. These signals are represented by a spatial activity pattern in M, which can also be encoded as an attractor.

The Response System (R): Conceptually, the Response System comprises two levels: 1) An *activation layer* that receives input from E, and has neurons specialized for each response element; and 2) A layer of actual response elements that perform the primitive functions associated with that element (e.g., simple reaching movements). In this paper, we show simulations only for the activation layer to focus on essential functionality. Typically, response elements would be fairly complex networks in their own right.

Encoding System Model

The E system is implemented as two layers of spiking neurons. The neurons use the Izhikevich model [39], which is computationally efficient and biologically plausible. The neuron equations are:

$$\frac{dv}{dt} = 0.04v^2 + 5v + 140 - u + I \quad (1)$$

$$\frac{du}{dt} = a(bv - u) \quad (2)$$

with resetting after each spike:

$$\text{if } v \geq +30mV, \quad \begin{cases} v \leftarrow c \\ u \leftarrow u + d \end{cases} \quad (3)$$

Here, v represents the membrane potential of the neuron, u represents a membrane recovery variable, which provides negative feedback to v , and a, b, c and d are parameter values that determine the neuron's intrinsic behavior. In particular, we use Izhikevich's class 2 excitability spiking model with $a=0.2$, $b=0.26$, $c=-65$, and $d=0$. The range of output spiking period is from 25ms to 2ms if the input level I changes from 0.4 to 24. Figure 2 shows the relationship between the stimulus input and the period of the spiking neuron.

As shown in Figure 1, the system has two layers conceptually. The first layer, termed the *input layer*, receives stimulus from upstream systems (e.g., prefrontal cortex), and has bidirectional connectivity with the output layer. The neurons in the second layer, called the *output layer*, are divided into several modules with dense internal connectivity. There are no inter-module connections in the current implementation. All neurons in each module are identical, but have different weights to the downstream system. As a result, the input from a module to its target in R can be varied depending on which neurons in the module are on or off.

Specific patterns of activity across both layers are stored in the E system as attractors, with the recurrent weights in the

input layer and the bidirectional weights between the two layers set by a Hebbian rule:

$$w_{ij} = \begin{cases} \frac{1}{N} \sum_{k=1}^P y_i^k y_j^k, & i \neq j; \\ 0, & \text{otherwise} \end{cases} \quad (4)$$

where w_{ij} is the weight of the connection from neuron j to neuron i , N is the number of neurons, P is the number of stored patterns, and y_i^k is the state of neuron i for the k^{th} pattern.

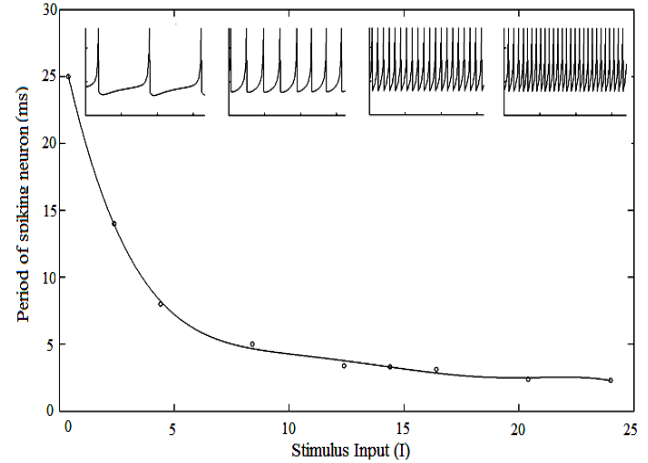


Figure 2: The relationship between the stimulus input and the period of spiking neuron. The inset graphs show neuron spiking at different input levels.

Each pattern is also heteroassociated with specific stimulus patterns through Hebbian learning. Given a brief stimulus, the network retrieves stored pattern most strongly associated with the stimulus and latches it until next stimulus. The output layer has significantly fewer neurons than the input layer, ensuring that correct retrieval in the latter is sufficient to trigger the correct output component of the attractor as well. In the simulations shown, the input and output layers have 400 and 100 spiking neurons, respectively. The output layer is divided into 10 modules, each with 10 neurons.

The excitatory input I^e and stimulus input I^s of neuron i at time t is given by:

$$I_i^e(t) = \sum_{j=1}^N \sum_n w_{i,j} \alpha(t - t_j^n - \Delta) \quad (5)$$

$$I_i^s(t) = \sum_{j=1}^N \sum_n w_{i,j} \alpha(t - t_{j(Stim)}^n) \quad (6)$$

where,

$$\alpha(t) = \frac{1}{\tau} \exp\left(\frac{-t}{\tau}\right) \quad (7)$$

N is the number of neurons, w_{ij} is the synaptic conductance from j to i , Δ is the synaptic delay, and τ is a time constant. The spike times of the j^{th} presynaptic neuron are denoted by t_j^n .

The input for neuron i at time t is:

$$I_i(t) = I_i^e(t) + I_i^s(t) \quad (8)$$

The attractors used for the current simulations are approximately orthogonal, each with about 9% neurons active. The stimulus duration is 20ms, after which the attractor is kept active purely through recurrent connections. Figure 3 shows the actual spiking patterns obtained in the output layer when the attractors 1 through 10 are triggered successively at intervals of 50ms.

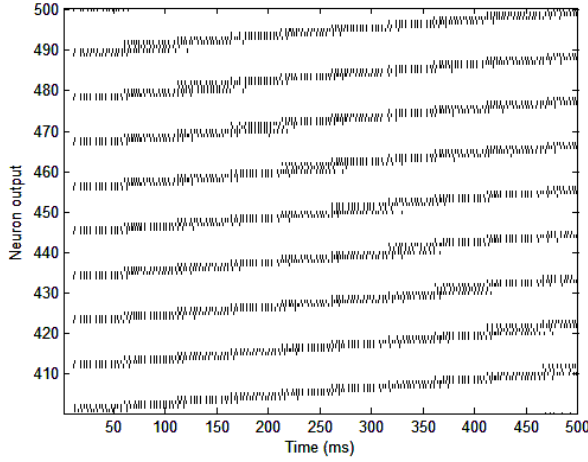


Figure 3: Spiking patterns of the output layer as the attractors are activated successively. The system has 10 near-orthogonal attractors, each of which remains active for 50 ms. Note that the number of active output layer neurons in each attractor varies, but the total number of active neurons across both layers is the same for all attractors.

Response System Model

The response system, R , has L modules of m neurons each corresponding to L different response elements. The neurons are modeled as modified RS (regular spiking) Izhikevich neurons [39]. The modification involves the inclusion of a modulated slow inactivation process that ensures that a neuron remains active only for a certain duration.

The neurons within each module are connected to each other through weak random inhibitory connections. Also all the neurons in the module are inhibited by neurons from other modules with strong inhibitory connections. When the modules are stimulated with inputs of different magnitudes, the module with the largest input is the first to reach firing threshold, and its activity inhibits all the other modules as long as it is active. However, the inactivation process ensures that the active module eventually turns off and the next most excited module can become active, thus producing the sequence.

The input to each module comes from neurons of the corresponding module in the output layer of the encoding system. The input to neuron j in module R_i of the response system is denoted by x_{ij} and is given by:

$$x_{ij}(t) = \sum_{k \in M_i} w_{ik} s_k(t) \quad (9)$$

where w_{ik} is the synaptic weight from the k^{th} neuron in attractor module E_i which projects to module R_i in the Response

System, and s_k is the spiking output of neuron k . Each neuron in E_i connects to all neurons in module R_i with the same weight, but the weight for each neuron in E_i is different. Thus, the total magnitude of stimulus from E_i to R_i neurons depends on which neurons in E_i are active in the current attractor in the E system. The input current to each neuron j in each group R_i is calculated as:

$$I_{ij}(t) = G(t) * x_{ij}(t) \quad (12)$$

where $*$ indicates the convolution operator and $G(t)$ is the synaptic double exponential kernel function given by

$$G(t) = \frac{\tau_1 \tau_2}{(\tau_1 - \tau_2)} \left(e^{-\frac{t}{\tau_1}} - e^{-\frac{t}{\tau_2}} \right) \quad (12)$$

where time to peak is given by

$$t_{peak} = \frac{\tau_1 \tau_2}{(\tau_1 - \tau_2)} \ln \frac{\tau_1}{\tau_2} \quad (13)$$

Each neuron's input is gated by a recurrent signal $g(t)$ based on the collective activity of its module. Also the input to each neuron is also gated by a *start signal*, $P(t)$, which tells the system to produce a sequence. Thus, the net input to each neuron in a group is represented by the equation:

$$I'_{ij}(t) = I_{ij}(t)g(t)P(t) + I''_{ij}(t)(1 - g(t)) \quad (12)$$

where $I''_{ij}(t)$ represents the recurrent input to the neuron and is given by

$$I''_{ij} = \sum_{j=1, j \neq i}^m w'_{ij} z'_{ij}$$

where m is the total number of neurons in a module, w'_{ij} is the recurrent connection weights within a module, and z'_{ij} is the current from each neuron in a group given by

$$z'_{ij}(t) = G''(t) * s_{ij}(t)$$

Here,

$$G''(t) = \frac{\tau_1'' \tau_2''}{(\tau_1'' - \tau_2'')} \left(e^{-\frac{t}{\tau_1''}} - e^{-\frac{t}{\tau_2''}} \right)$$

where $G''(t)$ is the transfer function of synaptic transmission from each neuron in a module to all the neurons in the same module, with time to peak is given by:

$$t_{peak} = \frac{\tau_1'' \tau_2''}{(\tau_1'' - \tau_2'')} \ln \frac{\tau_1''}{\tau_2''}$$

The gating input is defined as:

$$g(t) = \begin{cases} 1 & I''_{ij} \geq c \\ 0 & I''_{ij} < c \end{cases}$$

where c is a threshold defined such that when the current I_{ij}'' crosses it, the gating signal is set to 1 otherwise to 0.

The start signal $P(t)$ is defined as:

$$P(t) = \begin{cases} 1 & t \geq T_{start} \\ 0 & t < T_{start} \end{cases}$$

Thus, sequence generation begins after a duration T_{start} , which can be used to model delays such as those before a GO signal in delayed response tasks.

The dynamics of the membrane potential for neuron j in module R_i is given by:

$$\frac{dv_{ij}}{dt} = 0.04v_{ij}^2 + 5v_{ij} + 140 - u_{ij} + I_{ij}^{exc} - I_{ij}^{inh} \quad (14)$$

where I_{ij}^{exc} and I_{ij}^{inh} are the excitatory and inhibitory inputs, respectively, and u_{ij} , given by

$$u_{ij} = u_{ij}^q + f(u_{ij}^r) \quad (15)$$

represents the inactivation variable for the neuron. The first component, u_{ij}^q , is the standard inactivation variable in the RS model, while u_{ij}^r represents an activity-dependent inactivation variable representing the depletion of a resource needed for spiking. This variable increases only when the neuron spikes, and is modulated by a sigmoid function:

$$f(u) = \frac{\alpha}{1 + e^{-\beta u + \theta}}$$

where α , β and θ are parameters determining the effect of resource depletion on firing rate. The equation for u_{ij}^q is:

$$\frac{du_{ij}^q}{dt} = a(bv_{ij} - u_{ij}^q) \quad (16)$$

$$a = 0.01, \quad b = 0.26$$

$$v_{ij}(t) = c \quad \text{if } (v_{ij}(t) \geq 30) \quad (17)$$

$$c = -65$$

$$s_{ij}(t) = \begin{cases} 1 & v_{ij}(t) \geq 30 \\ 0 & \text{otherwise} \end{cases} \quad (18)$$

$$u_{ij}^q = u_{ij}^q + d \quad \text{if } (v_{ij}(t) \geq 30) \quad (19)$$

$$d = 2$$

$$u_{ij}^r = u_{ij}^r + r_i \quad \text{if } (v_{ij}(t) \geq 30) \quad (20)$$

where r_i indicates the resource depletion rate for each module, which is identical for all the neurons in a module, and s_{ij} indicates a spike of the j^{th} neuron in i^{th} module.

The inhibitory stimulus to neurons in R_i from all the other modules is

$$I_{ij}^{inh} = \sum_{\substack{k=1 \\ k \neq i}}^{N_m} w_{ij}^{inh} z_k \quad (21)$$

which is the sum of inputs, z_k , from inhibitory interneurons targeting group k , weighted by w_{ij}^{inh} with N_m denoting the total number of modules. The current from the inhibitory interneuron for module R_i is calculated as:

$$z_i(t) = G'(t) * s_{ij}(t) \quad (22)$$

$$G'(t) = \frac{\tau_1' \tau_2'}{(\tau_1' - \tau_2')} (e^{-\frac{t}{\tau_1'}} - e^{-\frac{t}{\tau_2'}}) \quad (23)$$

where $G'(t)$ is the transfer function of synaptic transmission from the inhibitory neuron to the neurons in the other modules, with time to peak is given by:

$$t_{peak} = \frac{\tau_1' \tau_2'}{(\tau_1' - \tau_2')} \ln \frac{\tau_1'}{\tau_2'} \quad (24)$$

IV. RESULTS

The system described above was implemented with several embedded response sequences. Figure 4 shows the recovery of one (especially simple) sequence when the attractor activated by the stimulus triggers response elements in the order of their indices. Figure 5 shows the result when the attractor pattern in E is the same as in Figure 4, but the activity pattern in M is different, causing response elements to have widely varying activity durations. Figure 6 shows two more response sequences generated by other attractor patterns in E. In each figure, the spikes generated are plotted as a raster pattern, with each spike indicated by a dot.

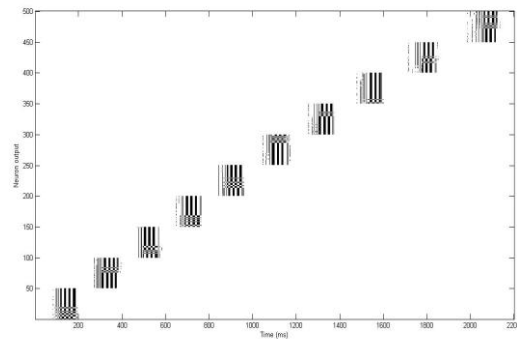


Figure 4: Generating a sequence where successive response groups are activated.

These figures clearly illustrate how static input patterns from the E and M systems can generate specific sequential responses. Stereotypical response sequences and their timing can be represented in the E and M systems as spatial attractor

patterns, and the system can generalize to variations of these responses (e.g., at different tempos) by systematically changing parts of the activity patterns in the E and M systems. This provides a convenient and efficient way to represent a large repertoire of response sequences involving the same response elements as a set of fixed-point attractors in E and M.

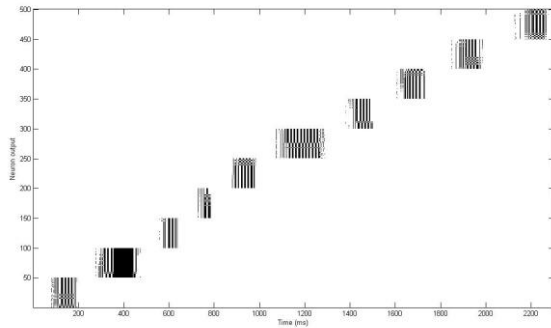


Figure 5: The same sequence as that in Figure 4, but with a different tempo. The E attractor is identical for the two cases, only the M pattern varies.

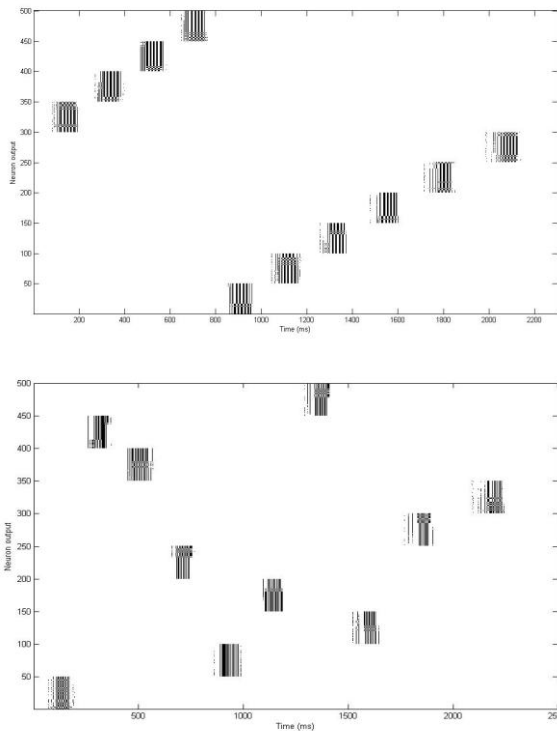
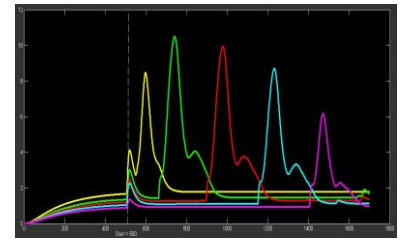
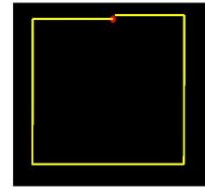
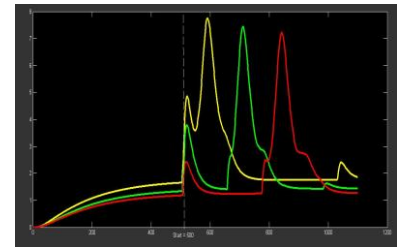
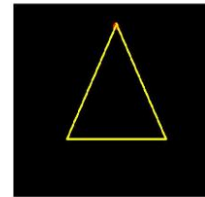


Figure 6: Sequences generated for two other attractors in the E system.

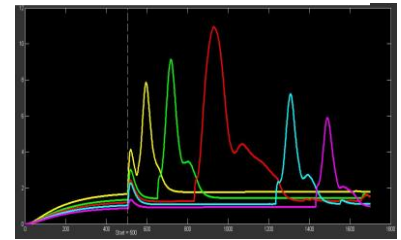
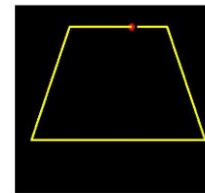
As an example, consider the case where the neurons in each R module encode for direction of hand movement [40], so that each sequence represents the tracing of a specific shape (e.g., a square). Once the shape has been learned as an activity pattern in E, variations (e.g., larger square, rectangles, etc.) can be produced simply by varying the activity pattern in M, while more complex variations (e.g., drawing the square backwards) could be encoded by varying the activity pattern in E.



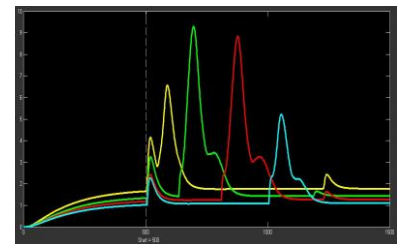
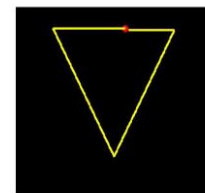
(a) Square



(b) Triangle



(c) Trapezoid



(d) Inverted Triangle

Figure 7: Left Column - Figures generated by four codes stored in the system when each response element encodes for movement in a certain direction. Right Column - Total activity time-series for E and R modules corresponding to each direction.

Figure 7 illustrates this with results from a simulation of the system producing four basic shapes. These were also used by Averbeck et al. to obtain their data showing that sequences are encoded by activity levels in the prefrontal cortex [34]. Each R module – and the corresponding E module – is assumed to represent one of 8 directions – the four cardinal directions and four intermediate ones. The right column in Figure 7 shows the activation strength of each representation, calculated as the total activity of the neurons in a module in R and its corresponding module in E. As shown in the figure, there is an orderly temporal evolution of each segment's representation.

Also the representation of each segment has a peak in the middle of the travel of each segment as seen in the experimental data. Our model does not reproduce the experimentally observed amplitude pattern of each segment as accurately as the LIST PARSE model [33], but doing so was not a consideration for us. The inclusion of a normalization process (as in [33]) can address this issue.

V. CONCLUSION

This paper has described a very simple spiking neuron model for representing stereotypical response sequences with specific timing using purely spatial codes. This allows for easy storage and recall of sequences, and the generalization of temporal codes over different variations in order and tempo. Such a system can provide the basis for constructing complex responses from simpler ones through development and learning – possibly by hierarchical composition of sequences using shorter sequential chunks as building blocks. It could also be useful in the representation and learning of elementary temporal constructs such as stereotypical actions, linguistic phrases or even abstract ideas with sequential structure.

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