

A Computational Model Of Episodic Memory Encoding In Dentate Gyrus Hippocampus Sub Region As Pattern Separator Using ART Neural Network

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ABSTRACT

This paper presents a computational model of encoding and separation of episodic events via Dentate Gyrus sub region of hippocampus. The proposed model is implemented using adaptive resonance theory (ART) neural network. The model incorporates the proposed method encoding of episodes in binary patterns. The proposed model is capable of achieving high level of pattern encoding and separation. The separation achieved for different episodes and events shown by the results are very good depending upon the vigilance parameter of the model. Vigilance parameter is assumed to be correlated to attention attribute while perceiving an episode of an event.

Keywords - Dentate Gyrus Computation, Episodic memory encoding, episode separation, ART network, hippocampus computational model.

I. INTRODUCTION

An episode is a series of related events. Intuitively, episodic memory is the memory of experiences, storing and recalling events including time and location. The hippocampus is an essential brain region in episodic memory, the storage and recall of series of events in space and time. Episodic memory is inherently related to the storage and recall of sequences of events. Episodes must be stored with one-shot learning, as humans and animals need not experience an episode many times to remember it. This storage and recall of sequences of events is hypothesized as a role of the hippocampus.

1.1 HIPPOCAMPUS

The hippocampus as well as its subregions are also referred to as cornu ammonis (CA), Ammon's horn, due to the intact hippocampus's hornlike shape. The hippocampus proper consists of two major sub regions: CA1 and CA3 [1]. The hippocampal formation includes the hippocampus proper, the dentate gyrus (DG), and the subiculum (and related structures)[2]. Between CA1 and CA3, resides a narrow sub region, CA2, which researchers generally ignore[5]. The subiculum, presubiculum, and parasubiculum are thought to be little more than an output relay from CA1 to various neocortical regions [6] [34-36], the neurons of the DG and CA regions: granule neurons, mossy neurons, pyramidal neurons, and inhibitory interneurons [3]. CA3 and CA1 pyramidal neurons have large somas and

branching apical and basal dendrites. Dentate Gyrus granule neurons have small somas and branching apical dendrites [3]. The DG has two excitatory neurons types: granule neurons and mossy neurons. Granule neurons are the only principal type in the DG, meaning only granule axons project out to other parts of the hippocampus (or brain). Mossy neurons are interneurons, the only known excitatory interneuron in the hippocampus. Granule neurons are small and densely packed in the granule layer of the DG, with their numbers estimated at about 1 million in the rat [5]. Their apical dendrites extend into the molecular layer; they have no basal dendrites. They spike only sparsely with about one-half of one percent of the population active during active behavior [4]. Their axons, mossy fibers, project both into the hilus (layer of the DG), connecting to mossy neurons apical dendrites, and into the CA3, driving pyramidal neurons; they drive inhibitory neurons in both areas as well. Inputs to granule neurons come from the perforant path (entorhinal cortex, layer II) and from the mossy neurons in the hilus.

The basic connectivity between regions of the hippocampus has long been known, the trisynaptic circuit. The basic schematic of hippocampal connectivity is a simple trisynaptic circuit that describes the connectivity among excitatory neurons between hippocampal sub regions (Figure1) [7]. In the trisynaptic circuit, axons from the perforant path fan out, innervating DG granule neurons (and CA3 pyramidal neurons).

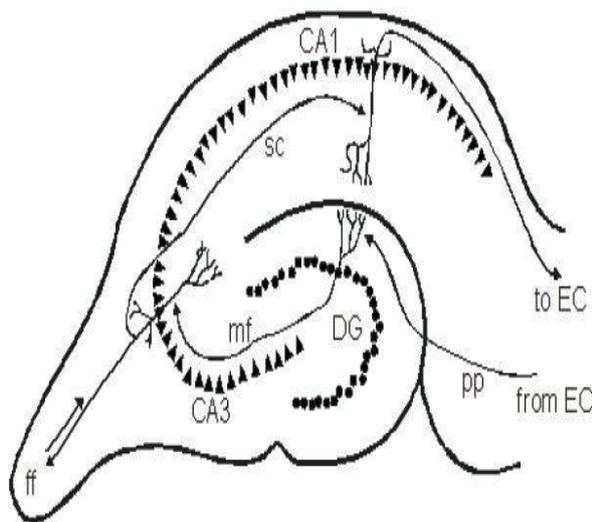


Figure1. The basic connectivity of the hippocampus is a trisynaptic circuit. Within a coronal slice, entorhinal cortex (EC) excites dentate gyrus (DG) granule neurons via the perforant path (PP). Granule neurons project their mossy fibers (MF) onto CA3 pyramidal neurons. CA3 neurons send Schaffer collateral (SC) axons to excite CA1 pyramidal neurons, the output of the hippocampus (to EC).[7]

Granule neurons project their axons (mossy fibers) onto synapses on CA3 pyramidal neurons. CA3 pyramidal neuron axons (Schaffer collaterals) fan out onto synapses on CA1 pyramidal neurons. Finally, CA1 pyramidal neurons project axons back to the EC. For a long period, neuroscientists assumed this simple circuit was responsible for all hippocampal processing, and although it provided a good starting point, it lacked many potentially important connections observed in the hippocampus both within each region and between regions.

1.2 LONG-TERM POTENTIATION AND DEPRESSION

Long-term potentiation (LTP) and long-term depression (LTD) are long-lasting (more than 30 minutes) increases and decreases in synaptic efficacy. LTP (and later LTD) was first discovered in the hippocampus [8]. The mechanics of LTP and LTD have been extensively studied but are only partially understood. The most studied synapse is the excitatory, glutamatergic Schaffer collateral synapse from CA3 pyramidal neurons to CA1 pyramidal neurons. Schaffer collateral (and many other types of) LTP and LTD are NMDA dependent. Many other types of LTP and LTD are independent of NMDA, such as one type from the mossy fibers onto CA3 pyramidal neurons.[3] When NMDA-receptor (NMDAR) gated synaptic channels are blocked by AP5, synapses resist both LTP and LTD [9]. NMDAR channels require both presynaptic input (glutamate) and postsynaptic depolarization to

relieve a magnesium block at hyperpolarized potentials. When the block is relieved by depolarization and the channel activated by glutamate, sodium and calcium flow into a synaptic spine head. Evidence suggests that calcium influx through NMDAR channels determines the sign of synaptic change. Low calcium influx results on average in no change, medium influx in depression, high influx in potentiation [9]. Calcium must flow through NMDAR channels; other sources are ineffective. Calcium triggers chemical cascades that add and remove (fast) AMPA-receptor (AMPA) gated channels to and from the synapse [10]. A lengthy list of neuromodulators, neuropeptides, and intracellular messenger molecules influence LTP and LTD, through their influence on calcium or by other means. A key molecule in the synaptic spine is CaMKII. Calcium acts on CaMKII, whose phosphorylation is necessary and possibly sufficient for LTP [10]. CaMKII is ideal for maintaining synaptic strength as it autophosphorylates. Once calcium drives phosphorylation beyond a threshold, CaMKII drives its own activation. Once the spine's calcium level decays back to baseline levels, models suggest CaMKII activation settles at one of two active levels, nearly completely phosphorylated or dephosphorylated [11]. Phosphorylated CaMKII is implicated in realizing LTP by (indirectly) inserting fast excitatory (voltage-independent) AMPAR gated synaptic channels into the spine membrane. In the hippocampus, depressed excitatory synapses include only NMDAR channels, whereas potentiated synapses include AMPAR channels as well [9]. The bistable activation of CaMKII suggests that excitatory synapses are binary; they include or exclude AMPAR channels. Recent observations support such a conclusion that individual synapses are binary weighted, depending on whether they express AMPA-gated channels [12], suggesting that graded synaptic strengths are merely a function of numerous synaptic contacts, some fraction of which are potentiated. On the other hand, the influence of numerous intracellular and extracellular processes, AMPAR and NMDAR channels' number, subunit types, and probability of presynaptic release, suggest that synapses are graded. For example, even if a synapse has inserted AMPAR channels, a reduced probability of presynaptic release would weaken the average effect of the synapse on the neuron. Also, debate continues as to whether LTP and LTD are two sides of the same process, both influencing AMPAR channels, or if they manifest in entirely different ways with one affecting the postsynaptic neuron and other the presynaptic one. Even with (fixed weighted) binary AMPAR expression, synapses are not truly off or on due to their NMDAR channels. NMDAR channels are effective, even in

the absence of AMPAR channels. Although synapses are often modeled as having binary weights, the presence of NMDAR channels at depressed excitatory synapses gives them the opportunity to drive the neuron anytime its membrane is depolarized. In fact, current through NMDAR channels is the dominant source of charge at excitatory synapses: The NMDAR channel's time constant (on the order of 100ms) is much longer than that of the AMPAR channel (a few ms). So even though its peak conductance is usually lower (at potentiated synapses), its influence is significant. Many induction protocols have been used to elicit LTP and LTD, including long high-frequency (100Hz) bursts for LTP and long low-frequency (5Hz) spikes for LTD. More recently LTP and LTD were found to be sensitive to spike timing.

1.3 HIPPOCAMPAL CIRCUITRY AND COMPUTATION

The unique multi-layered circuitry of the hippocampus, summarized in Figure 1, has intrigued computational neuroscientists interested in unravelling how the hippocampus achieves its unique encoding capabilities. Within the PHR(parahippocampal region), the EC is the major input and output region for the hippocampus. In the hippocampus proper, activity passes in turn through the DG and CA3 and CA1 fields—the so-called “trisynaptic circuit”(Figure3)—and back to the EC(Figure2). The principal cells of the DG greatly outnumber those of the EC[13], while having much lower activity levels [14][15]. Thus, mapping from the EC to the DG results in a highdimensional, extremely sparse neural code, likely due to the unique network of principal neurons and inhibitory neurons in the DG and adjacent hilar region [16]. The DG in turn projects to the CA3 field via mossy fiber synapses; during encoding, a sparse pattern of activation in the DG mandatorily causes a postsynaptic CA3 cell to fire[17][18]. DG—representing the mossy fiber synapses—are very sparse, but 100 times larger in magnitude than other weights in the circuit so that the dentate input dominates in the calculation of the CA3 activations during learning an episode.

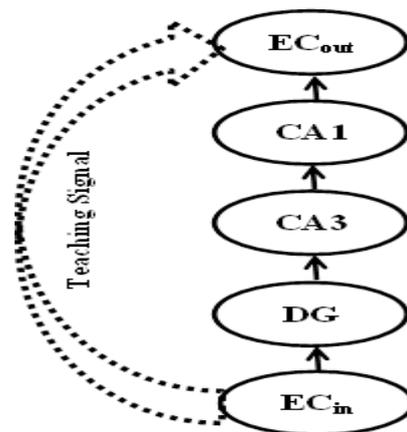


Figure2. Input of episodic pattern and processing schema of hippocampus sub regions

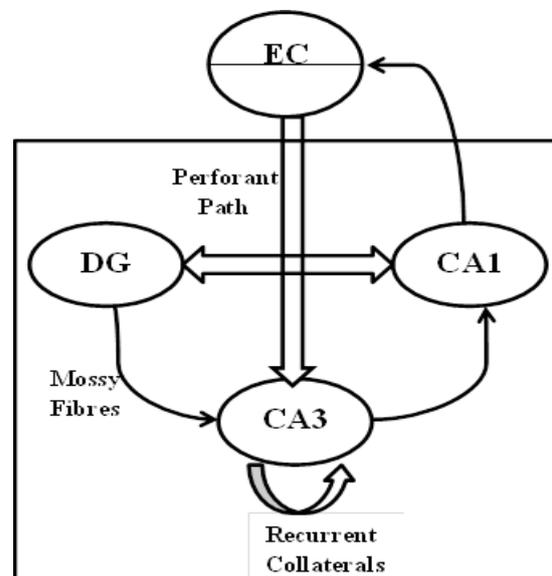


Figure3. Tri-synaptic circuitry of Hippocampus

The study episodic memory tasks, have emphasized the role of the hippocampus in the rapid encoding of episodic memories. Computational models play an important role in extending our understanding of the neural bases of learning and memory. By simplifying and isolating core principles of brain design, computational models help us understand which aspects of brain anatomy, circuitry and neural function are responsible for particular types of behavior [19]. In many episodic memory models, the hippocampal system is assumed to form relatively sparse patterns that overlap less than the input patterns from which they are formed [20][21]. The hippocampus is involved in encoding and integrating contextual information. Recently, it has been suggested that the dorsal dentate gyrus (dDG) hippocampal sub region may mediate the formation of contextual representations of the spatial environment through a conjunctive encoding process

whereby incoming multimodal information is integrated into a single higher-order representation [22]. DG encodes the episodic patterns to achieve higher separation and less interference [33]. Based on anatomical descriptions of the hippocampal formation, the DG provides the main input zone for the HPP and receives its major cortical input from the entorhinal cortex (EC) via the perforant pathway (PP)[23]. The EC inputs to the DG can be divided into a medial and lateral component [25]. The medial EC (MEC) input to the DG conveys spatial information and the lateral EC (LEC) input conveys no spatial information [24,25] It has been suggested that the DG may use a conjunctive encoding process to integrate multiple sensory inputs from medial and lateral portions of the EC into a single spatial representation [25]. In the present work a computational model of encoding and separation via DG sub region of hippocampus is presented.

II. MATERIALS AND METHODS

The artificial neural network model is presented in this paper(ART2 network) that simulates the role of Dentate Gyrus (DG) in episodic memory formation in the hippocampus.

In hippocampus formation input presented by HLCC to EC is fetched to the hippocampus formation (i.e. EC,DG,CA3,CA1and SC) regions through neuronal interconnections between their neuronal sub regions. The input presented by HLCC to EC is first encoded by EC and then fetched to DG during encoding and memorization process of episodes in episodic memory formation. The main task that is incorporated by DG is to encode and store the episodic patterns in such a way so that higher separation and minimum interference is achieved. DG works as pattern separator by detecting bindings in entities of an episodic pattern. The input episodic pattern from EC to DG is encoded using ALGO1proposed in this work . DG stores the encoded pattern in sparse manner and output of DG is then fetched to CA3 region which further memorizes the episodic pattern. The process encoding and memorization of episodic pattern by DG is presented in detail in this work.

In the present work the process of DG is modelled using ART2 ANN model which ia a specialised self-organising neural network capable of dealing with stability-plasticity dilemma of learning in neural networks. This is an unsupervised feed forward neural network which generates cluster centres for various episodic patterns presented to DG with minimum interference to achieve sparseness and higher separation between episodic patterns.

2.1 EPISODIC PATTERN ENCODING OF EC TO DG SYNAPSE INPUTS

In encoding the episodes it is assumed that in whatever manner the episode is sensed by sensory organs and perceived by brain, ultimately each episode can be represented in sentential form. The representation of episodes in sentential form is independent of how it is perceived such as visual, auditory or any other sensory inputs. In this work it is assumed that each episode is represented in sentential form comprising of episodic entities. Each episode comprises of entities, temporal and spatial information such as who, what, when, where, whom etc. The encoding scheme of the inputs received from EC and to be fetched to DG is described by ALGO1.

ALGO1. Episode Encoding

1. Represent episodic input of EC in sentential form.
2. Use 'b' bit representation of each letter in the sentence.

Where b is highest index in a language starting from 1.

e.g. in English language letters a-z are indexed from 1-26.

For space use \$ with index 0. And b bit representation

For English language b=5 as highest index 26 can be represented by 5 bits.

3. Pad each space between words of the sentential form with \$.
4. Set maximum number of connections to DG from EC to N_{max} .
 N_{max} = number of elements in input vector.
5. Count length(number of letters) of padded Episode $E_{count} = l_e$.
6. Encode in binary the padded sentential form of episode using b bits for each letter.
7. Append $(N_{max} - b * l_e)$ 0's in the end of each sentential episode to make each episode of equal length.
8. E_{pc} is final binary encoding of episode to be presented to DG.

Example:

Event: give

Input Episode: ram gave a book to sita yesterday

Padded Episode:

ram\$gave\$a\$book\$to\$sita\$yesterday

b=5

Nmax= 265

le= 33

(Nmax – b*le) = (265 – 5*33) = 100 0's appended

Output Encoded Episode Epc =

```

10010000010110100000001
11000011011000101000000
00010000000010011110111
10101100000101000111100
00010011010011010000001
00000110010010110011101
00001011001000100000011
10010000000000000000000
00000000000000000000000
00000000000000000000000
00000000000000000000000
00000000000000000000000
    
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To assure sparseness and lower interference an efficient encoding and memorization of events and episodes is required in DG. Any memory model of DG should be able to separate distinct events and episodes with a well-defined match scheme.[27]

In the present work the process of DG sub network is modelled using ART Neural network capable of solving the stability and plasticity dilemma[29-32]. The Model is implemented by ART2 ANN using Nmax input neurons. As in the proposed model each episode(episodic pattern) is represented as episodic pattern X a Nmax Dimensional binary vector. Nmax is generally taken equal to the highest length episode in the learning sample.(In this work Nmax=265, as highest length coded episode is of 265 bit long).The episodic patterns are presented through EC to DG (EC→DG).

2.2 DG ARCHITECTURE

DG is modelled by ART2 ANN which comprises of two layers of neuronal field F1 and F2. F1 is Input Field and F2 is category field. The input from EC is presented to F1 layer and neurons at F1 and F2 layer are connected in both way, bottom-up and top down manner. Number of neurons in F1 and F2 layers are equal to Nmax and total number of clusters(number of episodes to be encoded and memorized). As F1 and F2 layers are fully connected

through synaptic links in both way the link weights From F1 → F2 is denoted by Wij and that from F2 → F1 is denoted by Vji.

The vigilance parameter is most important regarding separation and minimization of interference between episodes. Higher the vigilance parameter value higher the separation and vise-versa. The Network parameters are as described in Table 2.

Following are the network inputs and architecture description:

Input vector: I=[x1,x2,x3,.....,xn]
 N=Nmax

Input Field: F1 layer of DG subnetwork works as input field. Number of neurons in F1 = Nmax

Category Field: layer F2 is category field. Number of neurons in F2 are taken to be maximum number of episodes to be encoded and memorized in DG sub network.

Node activation and competition: Nodes in F2 layer are activated according to the competition process. When a new episode is presented via F1 to F2 during competitive learning process the highest response node is selected among all the activated nodes. If the selected node qualifies the vigilance criteria. Then the wights are updated according to updating schema of uncommitted or committed node. If it fails in qualifying the vigilance criteria the second highest response activated node is selected and the process is repeated unless all activated nodes are checked. If no activated node is selected. A new node is set to be activated and weights are updated according to uncommitted node weight updating schema. The detailed process of weight updating is not discussed here. It can be referred in [28].

Dentate Gyrus(DG) is represented by above stated two layers F1 and F2. Synapses from EC → DG presents input to F1 layer neuron nodes of DG . The layer F1 presents the Input to F2 layer of DG. When resonance occurs the episodic pattern is encoded within DG and memorized with sufficient separation. The output of F2 is output of DG presented to CA3 region of hippocampus formation.

The episodic patterns thus encoded and memorized by DG are less correlated, highly separated, memorized in sparse manner and with lowest interference for higher value of vigilance parameter.

2.3 DATASET AND MODEL SIMULATION PARAMETERS

To simulate the DG process model presented in this work, total five events have been used. Episodes of various events comprises of ‘who’, ‘what’, ‘whom’, ‘where’, ‘when’ type of episodic information in various episodic patterns. Total

number of episodes and temporal categorization is shown in Table 1.

Table 1. Episodic events and episodes.

S. No.	Event	Temporal categorization of event	Number of episodes (samples)	Total number of episodes
1	give	gave	15	31
		Will give	16	
2	walk	walking	16	16
3	play	Will play	16	16
4	sing	singing	16	16
5	eat	ate	16	16
Total number of episodes(samples)				95

DG network parameter values used in this simulation are shown in Table 3.

Table 2. DG Subnetwork parameters (ART2-Network parameters)

S.N o.	Parameters	Description	Typical values	Actual values used in DG Network
1	n	Number of input units(dimension of input vector)	User defined	295
2	o	Number of cluster units (neurons at F2 layer)	User defined	95
3	a	Fixed weight in F1 layer	10	10(fixed)
4	b	Fixed weight in F1 layer	10	10(fixed)
5	c	Fixed weight used in testing for reset	0.1	0.1(fixed)
6	d	Activation	0.95	0.9(fixed)

		of winning F2 node		
7	e	Parameter to prevent division by zero when norm of vector is zero	Negligible value	0.000001(fixed)
8	θ	Noise suppression parameter	$1/\sqrt{n}$	0
9	α	Learning rate	User defined	Varying between [0 1]
10	ρ	Vigilance parameter	User defined	Varying between [0 1]
11	Vji(0)	Initial top down weights (F2→F1)	0	0
12	Wij(0)	Initial bottom up weights (F1→F2)	$Wij(0) < 1/(1-d)\sqrt{n}$	$0.5/(1-d)\sqrt{n}$

C and d should be chosen so that $c*d/(1-d) < 1$.

III. RESULTS AND ANALYSIS

In this paper we have presented an encoding algorithm for binary encoding of episodes being fetch from EC→DG. It is assumed that each perceived episode can be represented in sentential form of any language (here English language is used). Total number of letters are 26 having index from 1 to 26 for A to Z. for space \$ is used and index used for it is 0. As there are 27 total indexes for the letters being used in sentential representation of episode a 5-bit binary representation is used for each letter. A total of 5 events and 95 episodes are used to evaluate the model. While encoding the episodes used in this model using encoding algorithm presented in this paper highest encoded episode length is 265 bit binary string and that is the value of Nmax (i.e. Nmax =265). Rest of the episodes are of lesser length than 265. Hence, the difference bit number is padded with 0s to make the binary length of each episode equal to Nmax to achieve uniformity. Uniformly encoded episodic patterns are presented via EC to DG model presented in this paper.

The DG model is implemented by ART neural networks and parameters are as shown in Table 3. The episodes of all 5 events are presented to the DG network model proposed in this paper.

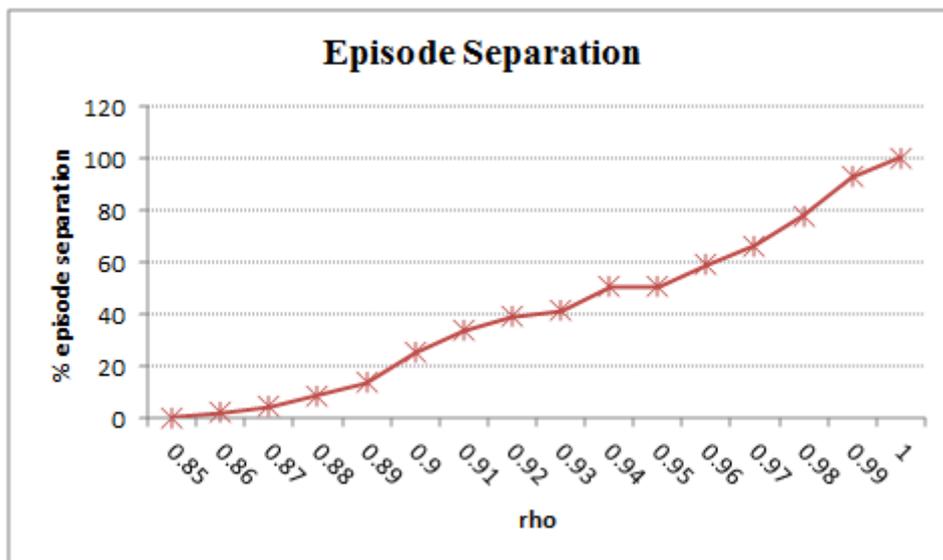


Figure 4. Episodic separation for different values of vigilance parameter

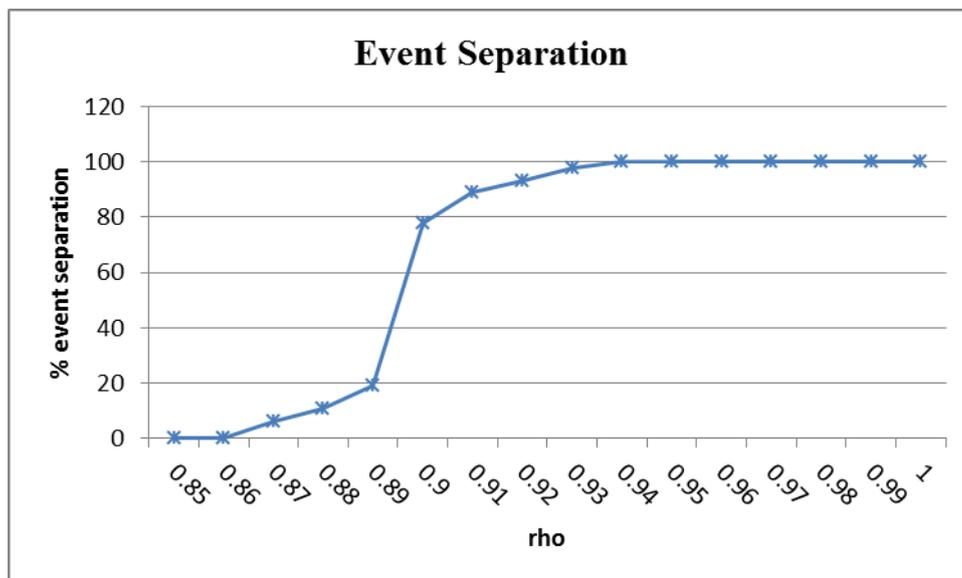


Figure 5. Event separation for different values of vigilance parameter

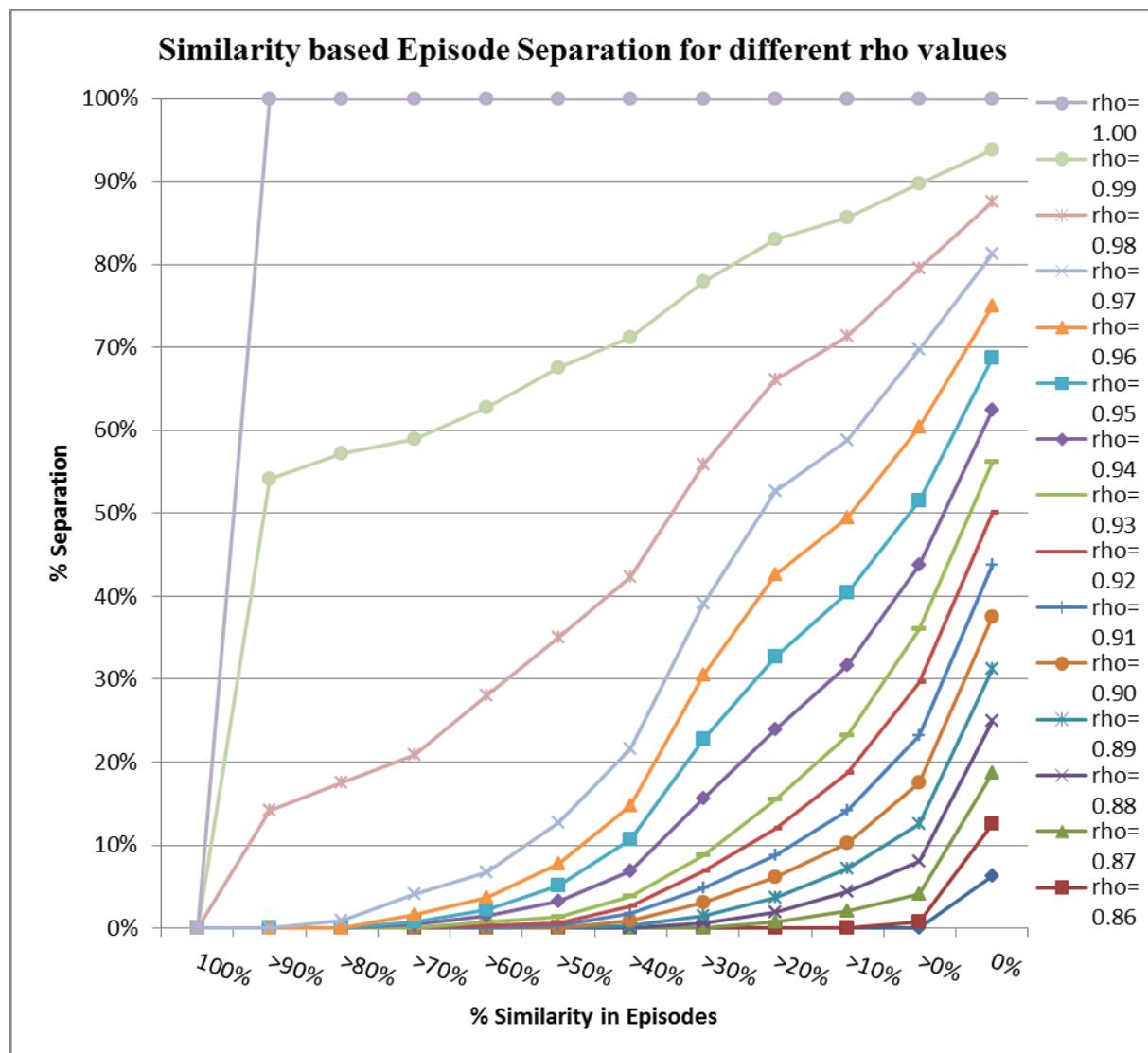


Figure 6. Episodic separation comparison for different values of vigilance parameter corresponding to similarity in episodes

The episode separation and event separations are analysed for different values of rho from [0,1], for rho value between 0 to 0.85, 0% separation is achieved independent of similarity between episodes or events. Hence we have shown the episodic and event separation for rho values between 0.85 to 1.

In Fig.4 the episode separation is shown for rho =0.85 to 1, independent of similarity between episodes. For rho values less than 0.9, % separation achieved is very low i.e. <15%. For rho values greater than 0.9 higher separation is achieved. Depending upon the similarities of episodes for higher values of rho from 0.9 to 1, higher separation and lower interference is achieved. As rho values is correlated to attention perceiving the episode, hence higher the attention, higher the separation in

episodes encoded and stored at DG subregion of hippocampus.

In Fig.5, The event separation is shown for rho=0.85 to 1 as lower values shows 0% separation in events achieved by DG model. The event separation for rho values less than 0.9 is very low < 20% but for values from 0.9 to 1 it is very high from 78% to 100% achieved by the DG model which even for low attentions events are well separated compared to episodes as achieved by the DG model.

In Fig.6, episode separation for rho values 0.85 to 1 is shown alongwith % similarity from 100% to 0% similarity, for rho values 0.85 to 0.94 for the similarity in episodes more than 50% the separation increases from 5% upto 60% for rho values from 0.85 to 0.94. For rho values higher than 0.94 to 0.97 for similarity in episodes greater than 80%, separation achieved almost 0%, for

similarity less than 80% and greater than 40% it is upto 20% and for lower similarity values it achieves 20% to 80%, separation for rho values from 0.94 to 0.97. For rho values from 0.98 to 1 the % separation achieved is high for similarity less than 90% which is 10% to 90% separation for rho value 0.98 for similarity less than 90% below to 0%. For rho value 0.99 for similarity less than 90% its value high upto 60% and almost similarly increases upto 95% for similarities less than 90% below to 0%. For rho value 1 except 100% similarity separation achieved is 100%.

Thus by the above results it is clear that separation achieved by DG model presented in this paper shows higher separation and low interface in DG encodes the episodes of various events with variable similarity and separation for lower to higher attention.

IV. CONCLUSION

In this paper we have used a new encoding scheme for episodes assuming that each perceived episode can be represented in sentential form of any language. Depending upon the language characteristic each episode can be encoded using the binary encoding scheme presented in this paper. The episodes encoded using this scheme is of uniform length. Here we have presented computational model of DG which is capable enough to incorporate the sparseness and separation capability shown by the DG sub region of the hippocampus. The model presented in this paper is dependent on the attention parameter. At appropriate value of vigilance parameter correlated to attention model is capable of separating events at lower values and episodes at higher values. In the future directions of work the work can be explored for other subregions of hippocampus as well as functionalities regarding episodic memory.

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