Adult Neurogenesis: Implications on Human And Computational Decision Making

Craig M. Vineyard¹, Stephen J. Verzi¹, Thomas P. Caudell², Michael L. Bernard¹, and James B. Aimone¹

¹ Sandia National Laboratories
Cognitive Modelling Department
Albuquerque, New Mexico, USA
cmviney@sandia.gov
Electrical and Computer Engineering Department
University of New Mexico
Albuquerque, New Mexico, USA

Abstract. Adult neurogenesis is the incorporation of new neurons into established, functioning neural circuits. Current theoretical work in the neurogenesis field has suggested that new neurons are of greatest importance in the encoding of new memories, particularly in the ability to fully capture features which are entirely novel or being experienced in a unique way. We present two models of neurogenesis (a spiking, biologically realistic model as well as a basic growing feedforward model) to investigate possible functional implications. We use an information theoretic computational complexity measure to quantitatively analyze the information content encoded with and without neurogenesis in our spiking model. And neural encoding capacity (as a function of neuron maturation) is examined in our simple feedforward network. Finally, we discuss potential functional implications for neurogenesis in high risk environments.

Keywords: Neurogenesis, Dentate Gyrus, Information Theoretic Complexity, Neural Network Modeling.

1 Introduction

Human cognition is facilitated by numerous forms of neuronal plasticity that span many different scales in both spatial and temporal dimensions. One such neural process that has received considerable attention over the past decade is adult neurogenesis, which is the incorporation of new neurons into established, functioning neural circuits [1]. Neurogenesis is uniquely limited to a few regions and has been shown to be regulated by a wide range of intrinsic and extrinsic behavioral conditions. The most studied neurogenic region is the dentate gyrus (DG) area of the hippocampus, a region known to be critically important for learning and memory.

Current theoretical work in the neurogenesis field has suggested that new neurons are of greatest importance in the encoding of new memories, particularly

in the ability to fully capture features which are entirely novel or being experienced in a unique way. This type of memory has the potential to be of critical importance in high consequence scenarios, in particular in situations where the decision-maker must base their reasoning on novel, previously unexperienced, aspects of the environment. Without the capability to properly encode and process novel components of an experience, a decision-maker may fall back on the familiar, which while often a proper strategy, can sometimes be detrimental.

We anticipate that this work can impact cognitive function in two distinct respects: 1) interventions that increase neurogenesis promise to be an effective method to improve acute decision making by individuals; and 2) computational approaches that implement neurogenesis-like plasticity and structural dynamics can potentially motivate a powerful new form of algorithms that can facilitate data processing and decision-making assistance in revolutionary ways.

In the following sections we will briefly describe the neurophysiology involved in neurogenesis and an associated encoding hypothesis, provide a real world high consequence decision making scenario with potential functional implications, describe two computational models to investigate neurogenesis, and provide some results analyzing these models.

2 Neurophysiology

Situated within the medial temporal lobe, the hippocampus is a well studied neural region that receives an amalgamation of sensory input signals and contributes significant functional importance such as its key role in episodic memory formation [2]. The dentate gyrus (DG) serves as an entry region of the hippocampus receiving sensory stimuli from both lateral and medial entorhinal cortex (EC) [3]. Although it is comprised of several cell types, granule cells are the most populous neuron types within the DG. The DG is a relatively large region (consisting of approximately 10 to 20 million neurons in humans), however it exhibits sparse activation meaning that only approximately 2 percent of these neurons are active at a given instance [4]. DG activity subsequently serves as input to the highly recurrent cornu ammonis 3 (CA3) region of hippocampus for further processing.

The sparse activation of the DG has often been attributed to a pattern separation functionality within DG [5]. From this perspective, the relatively few neurons firing despite the large size of DG corresponds to a unique non-overlapping encoding of the multi-modal sensory inputs from EC. Alternatively, another proposed role for DG is to control memory resolution [6]. From this perspective, young immature neurons are hyperexcitable and broadly respond to a wide variety of input stimulation. Mature neurons, on the other hand, are narrowly tuned to respond to specific inputs they have learned to selectively fire to. The integration of both mature and young neurons within the same neural network allows for a mixed coding hypothesis. From this perspective, the young, easily excitable neurons are integral for incorporating new memories within a neural network without interfering with existing encodings represented by the mature neurons.

3 Real World Scenario

As a real world example of a high consequence decision-making scenario with potential implications for neurogenesis, consider the role of the drone operator. Rather than piloting their aircraft internally from the confines of a cockpit, as conventional pilots do, drone pilots remotely operate their aircraft from a distant workstation with real time video feeds projected on computer screens. Some drones are equipped with weapons and are consequently able to take action if a hostile target is detected.

However, the majority of a drone operator's time is spent watching and surveying. According to Massachusetts Institute of Technology (MIT) aeronautics and astronautics professor Mary Cummings, "You might park a UAV over a house, waiting for someone to come in or come out, and thats where the boredom comes in" [7]. Despite the similar environment to that of a video game, a drone operator's shift is typically less action intensive. Instead, "...it is not uncommon in search and reconnaissance missions for a UAV pilot to spend the majority of the mission waiting for a system anomaly to occur, with only occasional system interactions" [8].

It is of crucial importance that this rare, anomalous event consisting of a target of interest appearing in what is an otherwise highly familiar environment does not go undetected. It is possible that highly active young neurons may facilitate the ability to encode and perceive this novel, but significant event.

4 Computational Models

To investigate the possible functional significance of neurogenesis we have developed two neural network models. The first is a large scale, biologically realistic, spiking neural network model. The second is a simple rate-coded feedforward network that grows new neurons and connections. In the following we will describe the two networks in greater detail.

4.1 Spiking Dynamics Model

We have developed a biologically motivated, spiking model comprised of nine cell types representing EC inputs as well the molecular layer, granule cell layer, and hilus of DG. The underlying neuron model we have implemented uses Izhikevich neural dynamics so that we can fit to actual electrophysiology data from mature and immature granule cells and hilar interneurons [9]. We have also incorporated biologically realistic ratios of neurons within the model. Particularly, we have experimented with a model consisting of 5,500 EC neurons and 50,000 DG granule cells. The EC neurons are split between lateral and medial EC providing object cell and grid cell inputs respectively.

The particular input firings are driven by a multi-context multi-day simulated experimental paradigm. In a single simulation day, the model is presented three different contexts consisting of a variety of items in various locations. Over the

course of multiple simulation days, the first context is the same every day and is repeatedly presented to the model as a very familiar input. The second input presented each day is familiar context that the model has been presented before, but not as frequently as the first very familiar input. And finally, the third input presented each day is a novel, formerly unseen input (although it may consist of some formerly seen items in new locations and paired with different combinations of items). This experimental paradigm allows the model to investigate both acute and long term effects of neurogenesis while varying neurogenesis rates in a controlled manner.

4.2 Basic Neurogenesis Model

Additionally, to investigate fundamental neurogenesis functionality, such as the mixed coding hypothesis, we have also implemented a basic feedforward model which relaxes biological realism. This simplistic model consists of two layers of neurons. A fixed size input layer representing the EC, and a growing layer of DG granule cells.

The EC layer consists of both excitatory and inhibitory inputs, with four times as many excitatory as inhibitory inputs. Both the excitatory and inhibitory neurons exhibit a twenty percent activation each timestep. Over time, the DG layer grows both by incorporating new neurons as well as adding additional synapses (both excitatory and inhibitory) to the existing neurons as they mature. Just as there are more excitatory inputs than inhibitory, there are likewise more synapses to excitatory inputs than inhibitory. However, the inhibitory synapses have a stronger effect than the excitatory synapses. Throughout the neurogenesis network growth process, these ratios are preserved.

As a simplistic model of neural behavior, DG neurons fire if for a given timestep, input excitation exceeds input inhibition. This basic behavior is subsequently regulated by Hebbian learning such that if an input causes a DG neuron to fire, its synapses are updated accordingly.

Over time, new neurons are added to the DG layer. Each of these new neurons is randomly connected to the EC inputs, with a baseline amount of synapses. Additionally, over time, all neurons incorporate new synapses until they reach full maturity which happens when synaptic connections to the EC inputs reach twenty percent (of all available EC inputs). Throughout this temporal maturation process, a set of EC inputs are cycled through. Rather than exposing all of the inputs to the full input set, instead subsets of the inputs are presented during certain time windows.

For a more detailed description of this model please see [10].

5 Results

To quantitatively assess the potential benefits to neurogenesis we have analyzed computational complexity as an estimation of information representation from an information theoretic standpoint as well as examined neuronal encoding rates. The results of these analyses for our two computational models are presented next.

5.1 Computational Complexity of the Spiking Dynamics Model

To analyze the encoding capability of our spiking dynamics model we looked at the computational complexity of the granule cell neural ensemble over the course of the presentation of a particular context. Shannon entropy is a fundamental approach to quantize the amount of information in a variety of sources such as communication channels [11]. Additionally, many approaches have been devised to apply this sort of information measure to neurons [12]. However, doing so requires knowledge of the firing behavior probability distribution for the neurons within the model.

Rather, in lieu of estimating neuron firing probabilities, we have used complexity as a measure of compressibility in order to estimate entropy to quantitatively assess the information content of a signal. Szczepanski et al. applied the general Lempel-Ziv complexity (LZ-Complexity) measure to estimate entropy of real and simulated neurons [13]. But unlike the work of Szczepanski et al., rather than applying LZ-Complexity analysis to individual neuron spike trains, we have applied the approach to a neural population as a whole. LZ-Complexity is based upon measuring the rate of generation of new patterns along a sequence of characters in a string being compressed [14]. Applied to neuron spike trains, this technique looks for repeated spiking behavior over time. Instead, by applying it across an entire neural ensemble, we assessed repeated patterns of neural co-activity. Synaptic modifications alter the firing behavior of the neural network through learning. In order to account for this plasticity of the network, rather than computing the ensemble complexity at each timestep, we concatenated all of the firing outputs of the entire neural ensemble (while presented a single input context) into a long spike signal. This approach is depicted in Fig. 1.

Once the spike signal is converted into a binary signal, where an action potential is encoded as a one and the absence of activity by a zero, the normalized complexity may then be computed as follows:

$$c_{\alpha}(x^n) = \frac{C_{\alpha}(x^n)}{n} * log_{\alpha}n.$$
 (1)

Normalized complexity measures the generation rate of new patterns along a word of length n with letters from an alphabet of size α (in this case two). Additionally, it can be proven [11] that as the string length (our series of neural firings in this case) goes to infinity, the supremum of the normalized complexity approaches the entropy of the signal S:

$$\lim_{n \to \infty} \sup c_{\alpha}(x^n) \le H_{\alpha}(S). \tag{2}$$

We have implemented two instantiations of a biologically inspired spiking neural model, each consisting of 50,000 granule cells. The difference between these two

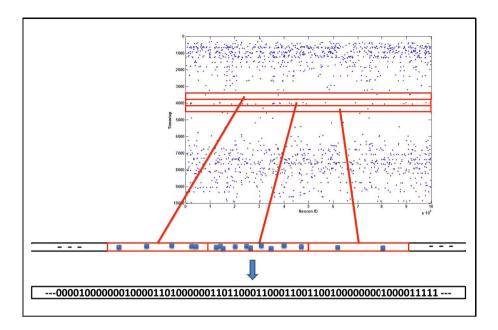


Fig. 1. Concatenation of neural firings across the population ensemble to generate a binary spike signal preserving temporal synchrony.

models is that the first does not implement neurogenesis while the second has a ten percent neurogenesis rate. Both models were exposed to three contexts across different simulated days as described formerly in the model description. Fig. 2 depicts the normalized complexity values for these two models across seven days of contexts (with the three numbers corresponding to normalized complexity for each of the three contexts, respectively). As evident by Fig. 2, the neural network with neurogenesis exhibits a distinct increase in information content, quantitatively inferred by means of normalized complexity, compared to the network with no neurogenesis across all days and contexts.

	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6	Day 7
No NG	0.000003 0.000003 0.000003	0.000002 0.000002 0.000003	0.000002 0.000002 0.000002	0.000002 0.000002 0.000003	0.000002 0.000002 0.000002	0.000002 0.000003 0.000002	0.000002 0.000002 0.000002
10% NG	0.000032 0.000031 0.000031	0.000033 0.000035 0.000033		0.000898 0.000846 0.000748	0.000789 0.000872 0.000824	0.001201 0.000458 0.000676	0.001250

Fig. 2. Normalized Complexity values for 50,000 granule cell network with zero and ten percent neurogenesis over seven days of varied contexts

5.2 Basic Neurogenesis Model

In evaluating our basic neurogenesis model, we experimented with an EC size of 12,500 neurons (10,000 excitatory and 2,500 inhibitory inputs). The EC layer itself had no input, however the patterns of activity we specified for it at a given timestep served as the inputs for the DG layer. The EC does not receive direct sensory input, but rather receives signals which have been pre-processed, such as by the visual cortex. Alternatively, specific input patterns such as visual images could be applied as inputs to the model if an appropriate neural sensory processing function (such as a hashing function) were used to process the raw input. Such a framework is illustrated in Fig. 3, where we have currently only implemented the portion to the right of the human comprehensible images in the figure, with binary EC activation patterns and a growing network of DG neurons.

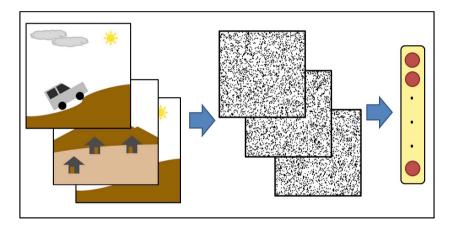


Fig. 3. General framework of a basic neurogenesis model proceeding from input images to an entorhinal cortex distributed representation and subsequent processing by a growing dentate gyrus network

In our analysis, we varied the maximum allowed growth in the DG layer to investigate network plasticity as well as learn-ability. In all cases, the younger immature neurons proved to be more excitable and responsive to a greater number of inputs despite having fewer connections than the more mature neurons. And likewise, the older neurons, through maturation, became narrowly tuned and responsive to specific input stimuli. This behavior is evident in Fig. 4 where the horizontal axis delineates the particular neurons by maturation age and the vertical axis represents the number of inputs each neuron responds to. The neurons in the figure are ordered by when they were added to the network, so the older (more mature) neurons which were added first are on the left and the younger more recently added neurons are on the right. To account for variability

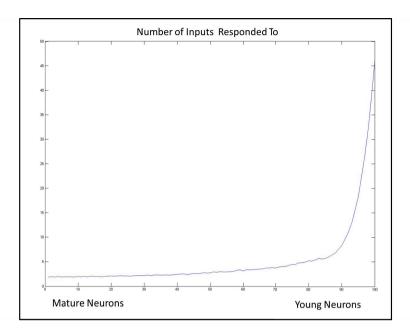


Fig. 4. Number of input patterns each neuron responds to. Moving from left to right represents the ordering in which new neurons were added to the network such that the rightmost neurons are the youngest neurons.

in the random synaptic connectivity, the number of inputs the neurons respond to are averaged over 1000 simulation runs of the model.

Furthermore, informal evaluations have also shown that given a sufficient neurogenesis rate in conjunction with an adequately sized DG proved to be sufficient to encode all inputs. This characteristic is important for network stability such that as neurons within the network mature and become tightly tuned to specific inputs that prior information is not lost in exchange for the novel stimuli. In this sense, the mature neurons are selectively responsive to narrowly tuned inputs but do not respond to novel stimuli. We evaluated this functionality by turning off Hebbian learning and re-showing the network the formerly seen inputs as well as a set of novel inputs. The mature neurons only responded to their select inputs while the younger neurons were responsive to novel stimuli as well as the formerly seen inputs.

6 Conclusions

Through neurogenesis, it appears that the incorporation of new cells within a neural circuit may be a means to increase the information content of the network as well as provide a means to encode novel stimuli. New neurons, which are highly excitable, have an increased likelihood of encoding current stimuli.

Consequently, as they mature they become more tightly tuned to particular inputs being learned and are not as easily able to incorporate the novel stimuli into the network without neurogenesis. Such a phenomena may play a crucial role in high consequence decision making scenarios such as that of a drone operator. On a surveillance mission, the majority of the images a drone operator sees may be routine and familiar if they have surveyed the same area previously. The scenario may be entirely familiar if nothing has changed regarding the area under consideration. Or it may be a highly familiar scene in which all of the usual components are there but a suspect's vehicle is parked on the other side of the house for example. However, it is of utmost importance in this domain to be cognizant of the subtle change in which a key target appears in what was an otherwise routine surveillance so the situation can be properly assessed and the appropriate action taken. A better understanding of the neurogenesis phenomena and its functional implications may allow for this capability to be increased, or alternatively incorporated within computational tools as an aid leading to improved human performance.

While the potential benefits adult neurogenesis may provide are exciting, its functional implications are still far from understood. As future work, we plan to investigate the effects of varying neurogenesis rates, examine whether the maturation rate has any effect on learnability or stability, study strategies for synaptic growth/formation, and consider neuronal death as a contrasting balance to neurogenesis. Additionally, we also plan to investigate possible application areas which may benefit from neurogenesis like mechanisms such as memory management, computational encoding schemes, and dynamic decision making.

Acknowledgements. Sandia National Laboratories is a multi-program laboratory managed and operated by Sandia Corporation, a wholly owned subsidiary of Lockheed Martin Corporation, for the U.S. Department of Energys National Nuclear Security Administration under contract DE-AC04-94AL85000.

References

- Aimone, J.B., Jessberger, S., Gage, F.H.: Adult Neurogenesis. Scholarpedia 2(2) (2100)
- Eichenbaum, H.: The Hippocampus and Declarative Memory: Cognitive Mechanisms and Neural Codes. Behavioural Brain Research, 199–207 (2001)
- Suzuki, W., Eichenbaum, H.: The Neurophysiology of Memory. Annals of the NY Academy of Sciences, 175–191 (2000)
- Andersen, P., Morris, R., Amaral, D., Bliss, T., O'Keefe, J. (eds.): The Hippocampus Book. Oxford University Press, USA (2006)
- O'Reilly, R.C., McClelland, J.L.: Hippocampal Conjunctive Encoding, Storage, and Recall: Avoiding a Trade-Off. Hippocampus 4(6), 661–682 (1994)
- Aimone, J.B., Deng, W., Gage, F.H.: Resolving New Memories: A Critical Look at the Dentate Gyrus, Adult Neurogenesis, and Pattern Separation. Neuron. 70(4), 589–596 (2011)

- 7. MIT news: Driving drones can be a drag, http://web.mit.edu/newsoffice/2012/boredom-and-unmanned-aerial-vehicles-1114.html
- 8. Cummings, M.L., Mastracchio, C., Thornburg, K.M., Mkrtchyan, A.: Boredome and Distraction in Multiple Unmanned Vehicle Supervisory Control. Interacting with Computers 25(1), 34–47 (2013)
- 9. Izhikevich, E.M.: Simple Model of Spiking Neurons. IEEE Transactions on Neural Networks 14(6), 1569–1572 (2003)
- Li, Y., Aimone, J.B., Xu, X., Callaway, E.M., Gage, F.H.: Development of GABAergic Inputs Controls the Contribution of Maturing Neurons to the Adult Hippocampal Network. Proceedings of the National Academy of Sciences 109(11), 4290–4295 (2012)
- 11. Cover, T., Thomas, J.: Elements of Information Theory. Wiley, New Jersey (2006)
- Victor, J.D.: Approaches to Information-Theoretic Analysis of Neural Activity. Biological Theory 1(3), 302–316 (2006)
- Szczepanski, J., Amigo, J.M., Wajnryb, E., Sanchez-Vives, M.V.: Application of Lempel-Ziv complexity to the analysis of neural discharges. Network: Computation in Neural Systems 14, 335–350 (2003)
- Lempel, A., Ziv, J.: On the complexity of an individual sequence. IEEE Transactions on Information Theory IT-22, 75–88 (1976)