Center for Computing Research

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Sandia National Laboratories

Quantifying Adult Neurogenesis with Implications for Computation

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U.S. DEPARTMENT OF ENERGY

National Nuclear Security Administration

LABORATORY DIRECTED RESEARCH & DEVELOPMENT

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Computational Modeling & Analysis

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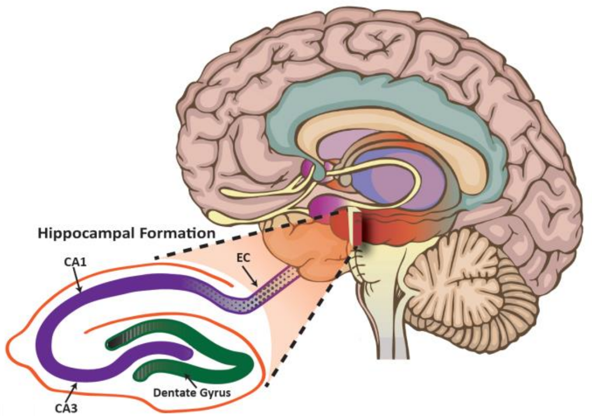
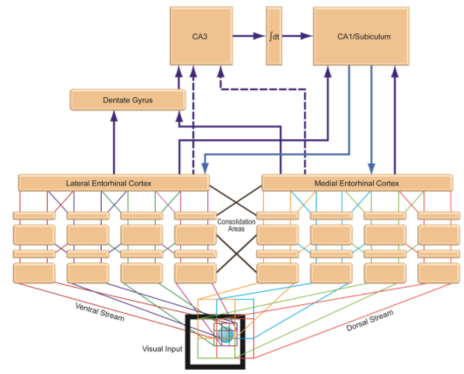
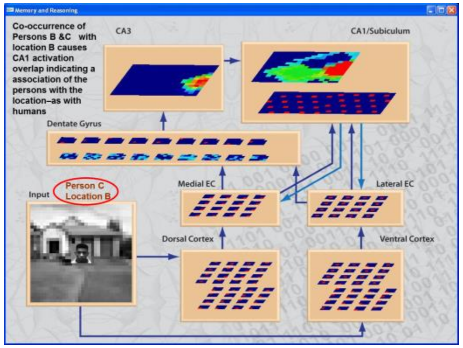
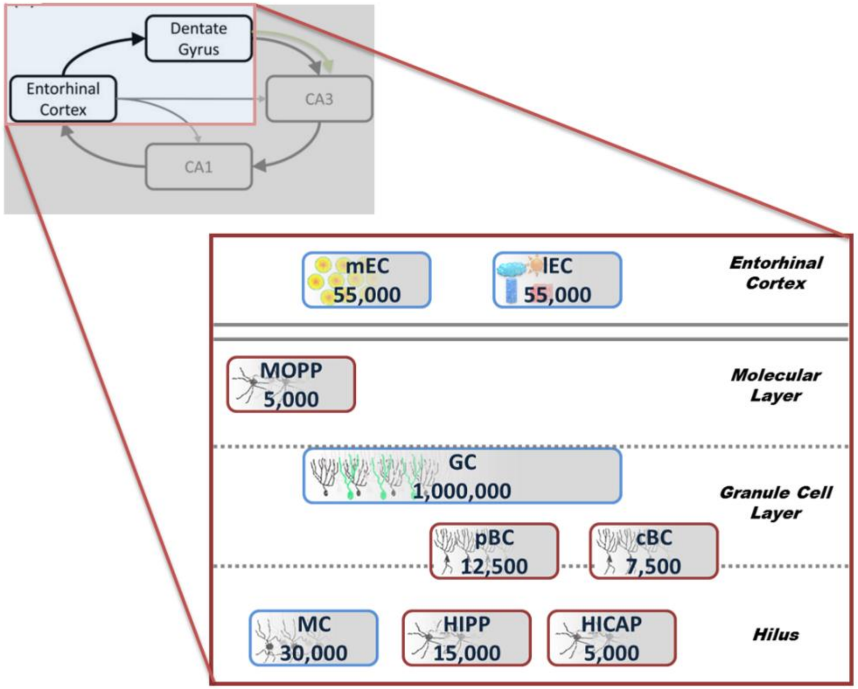
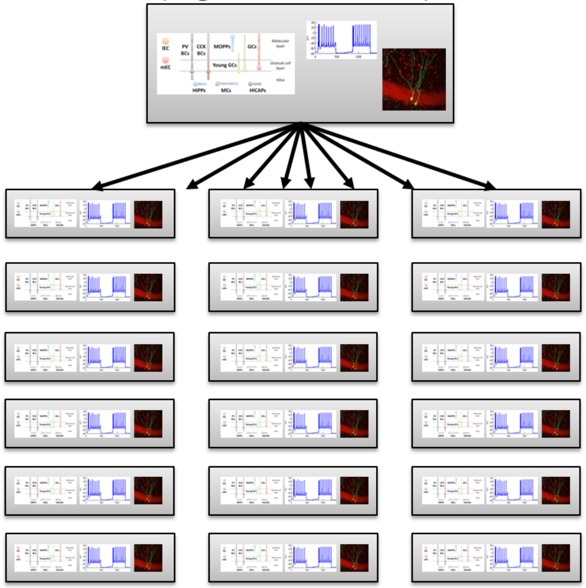








Full Model
(e.g., 1 million GCs)



Each node contains fraction of neurons
(e.g., 2,000 GCs)

What is Information?

- Information theory provides entropy of a discrete random variable as a quantitative measure of information

$$H(X) = \sum_{x \in X} p(x) \log(\frac{1}{p(x)})$$

- The intuitive idea behind Shannon's measure is that the more surprising a message is, the more information it conveys.
  - Ex: If I tell you that none of you will win the lottery tomorrow, this is not very surprising. But if I say that one of you will, this is very surprising indeed, and in some intuitive sense more informative.

- So what?

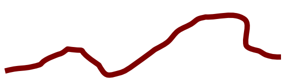
Applicability to Neuroscience

- Can be applied to neuroscience to quantitatively measure the information content of firing neurons.
  - And it has been with various methods such as:
    - Plug-in Entropy, Jackknife debiased, Asymptotically debiased, Ma bound
    - Bayesian/Dirichlet prior, Coverage-adjusted, Best upper bound, …
- But there are issues…
  - Entropy (and many other concepts from information theory) calculations require knowledge of the firing behavior probability distributions for the neurons - however
    - Limitations to in vivo recording capabilities
    - Neurons are somewhat deterministic
    - Neural plasticity effectively creates non-static distributions
    - Applicable to single neurons but not ensembles

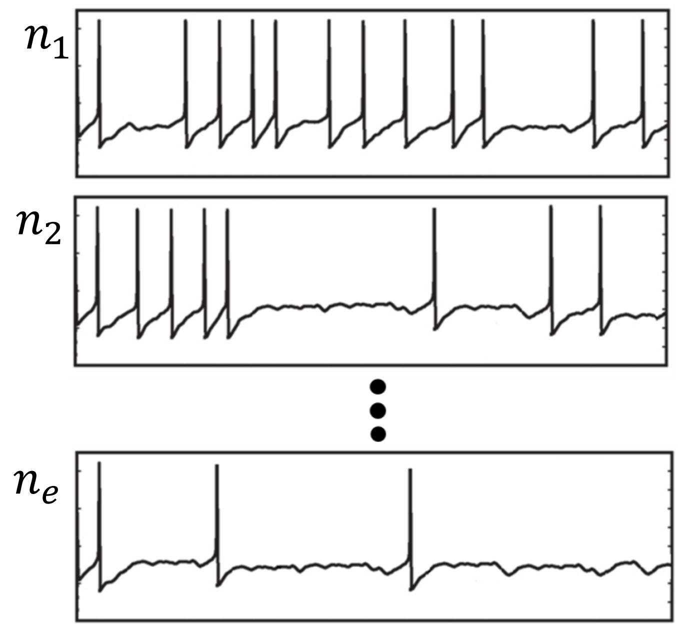
Neural Transform

Neural Ensemble Information Content

$N(t)$



$T(N)$



$C(T(N))$

$\sim H(N(t))$

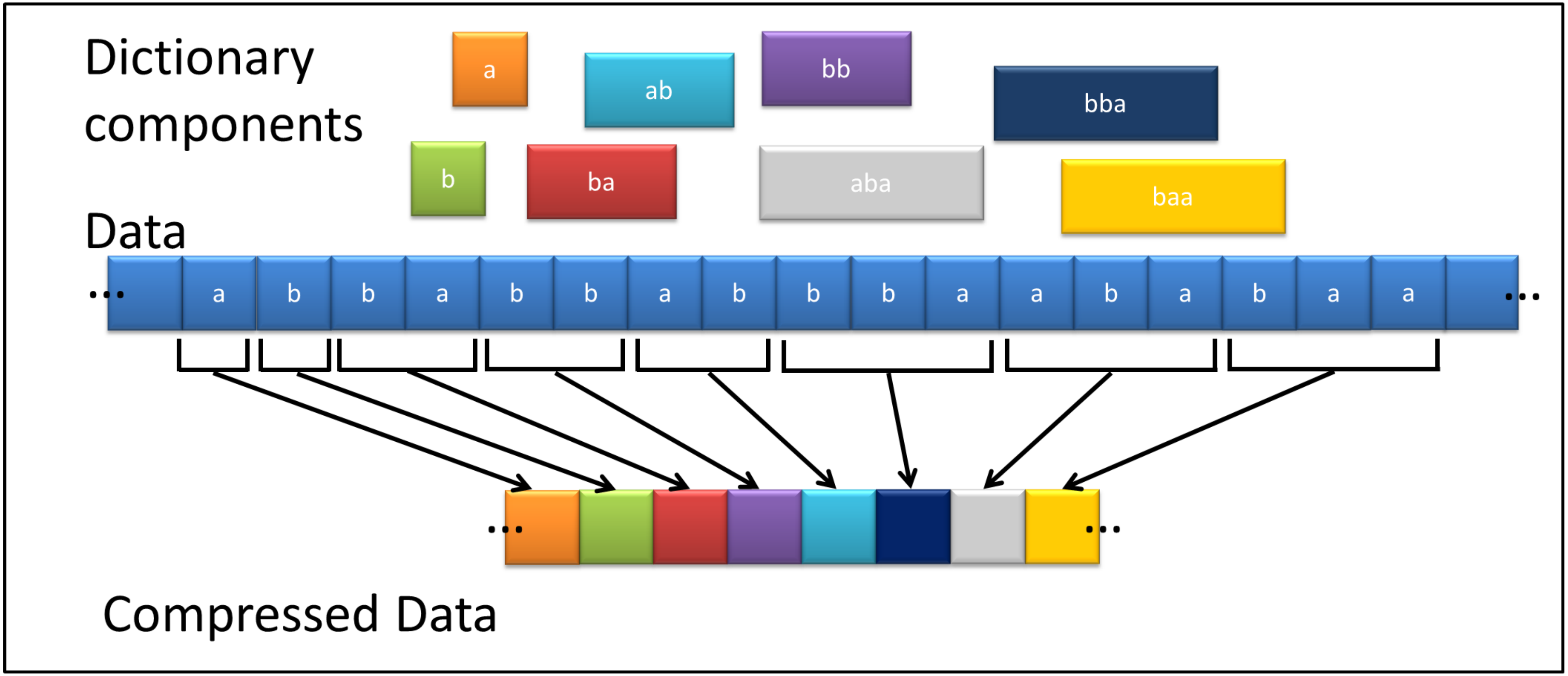
Approximation of Neural Ensemble Information Content

Compression

- Use complexity as a measure of compressibility in order to estimate entropy to quantitatively assess the information content of a signal.

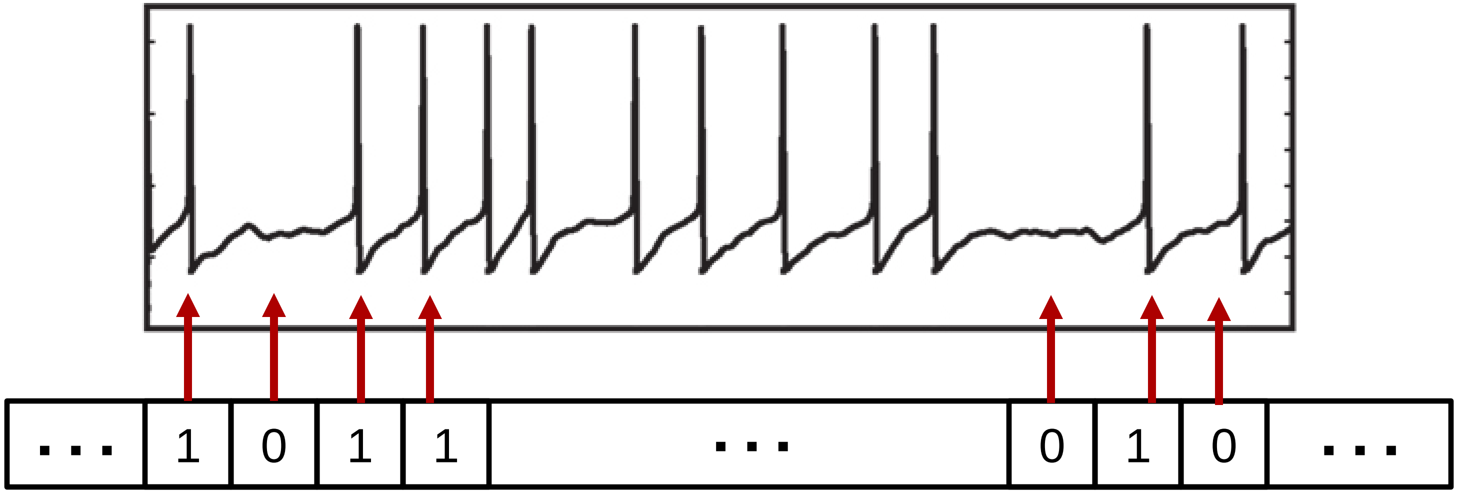
- Szczepanski et al. applied the general Lempel-Ziv complexity (LZ-Complexity) measure to estimate entropy of real and simulated neurons.
- LZ Compression is a dictionary technique that does not require a probabilistic model.
  - Rather dictionary compression techniques exploit redundancies in the data.
  - LZ compression has been used in applications such as UNIX compress command and GIF compression.

LZ 78 Example



Compression

- LZ-Complexity is based upon measuring the rate of generation of new patterns along a sequence of characters in a string being compressed.
- Applied to neuron spike trains, this technique looks for repeated spiking behavior over time.



Compression

- 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:

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

- 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).

Compression

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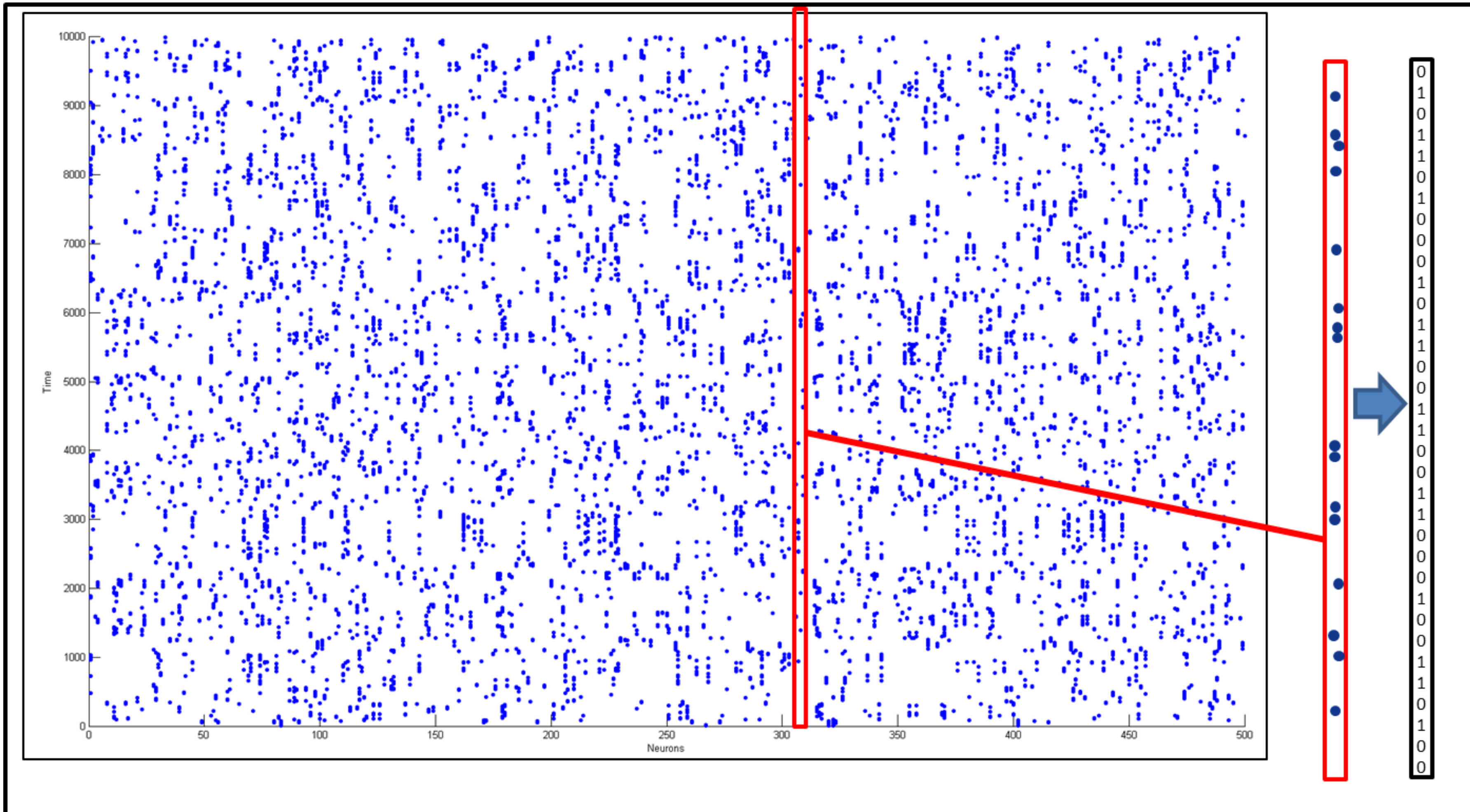
- But unlike the work of Szczepanski et al., rather than applying LZ-Complexity analysis to individual neuron spike trains, we have applied the approach to a neural population as a whole.

- It can be proven that as the string length goes to infinity, the supremum of the normalized complexity approaches the entropy of the signal S:

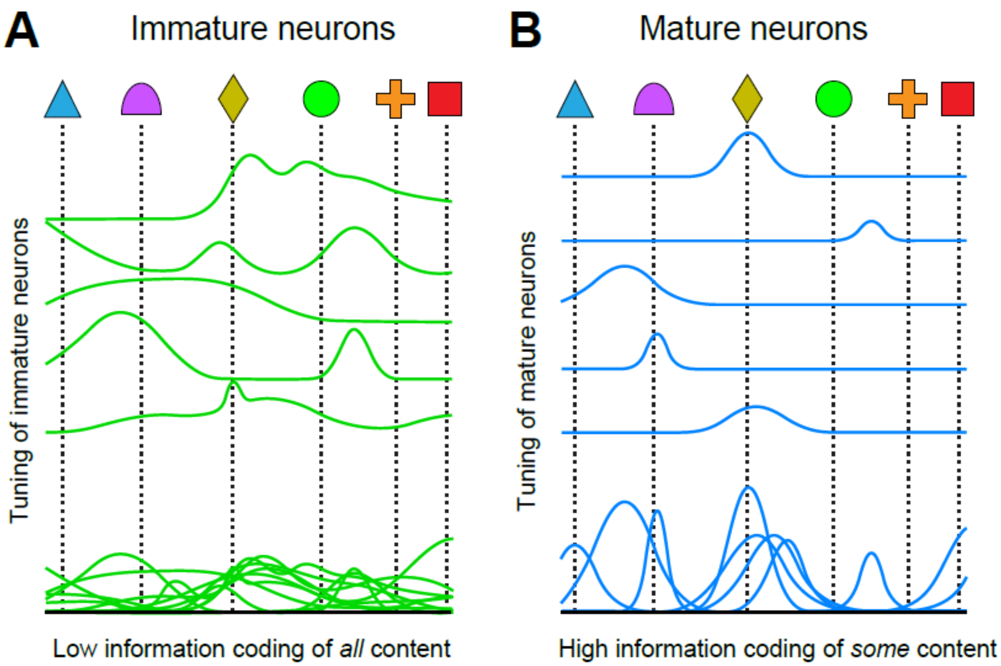
$$\lim_{n \to \infty} \sup c_{\propto}(x^n) \leq H_{\alpha}(S)$$

Spike Illustration



Mixed Coding

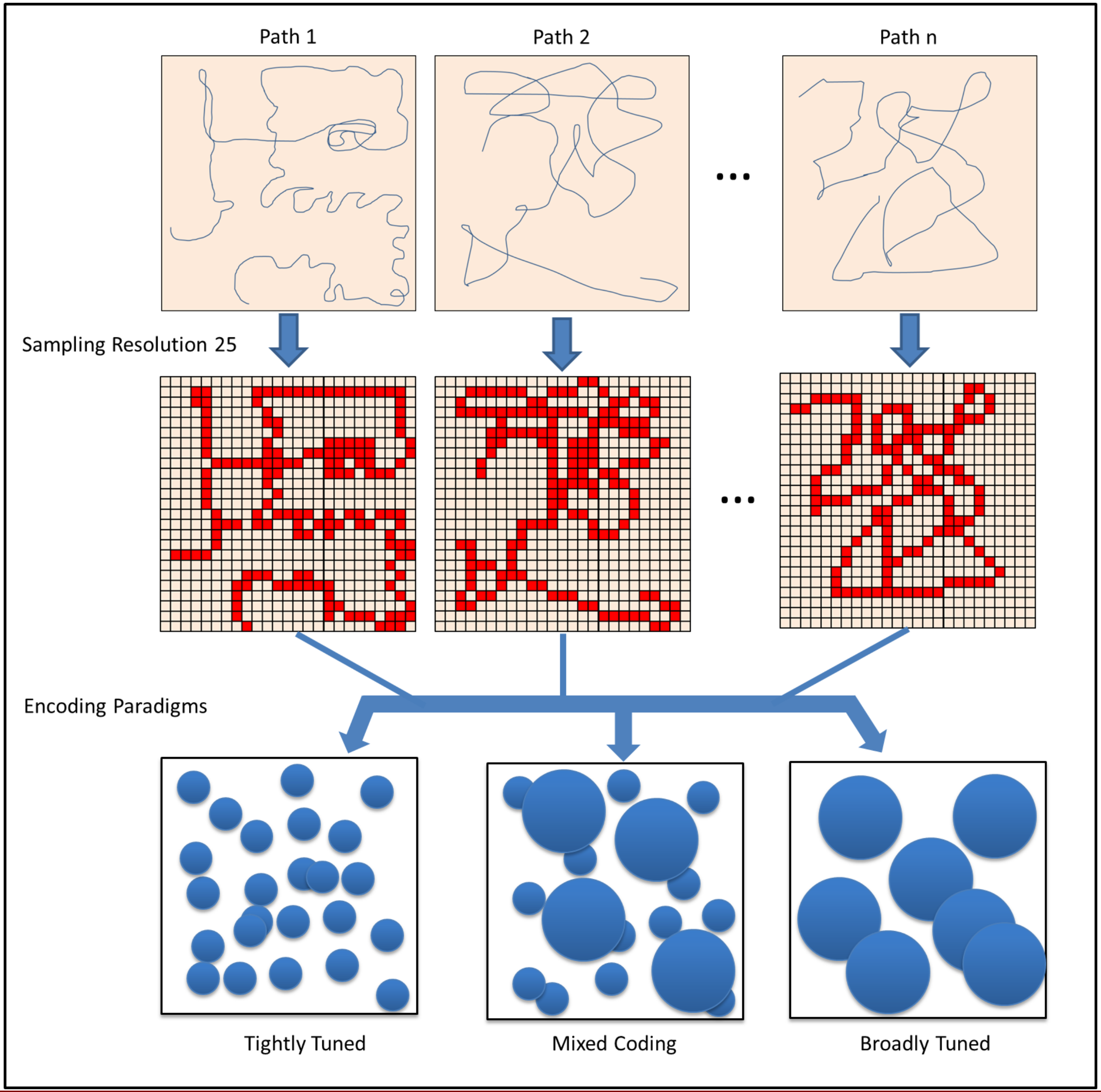
Immature and mature neurons encode information differently



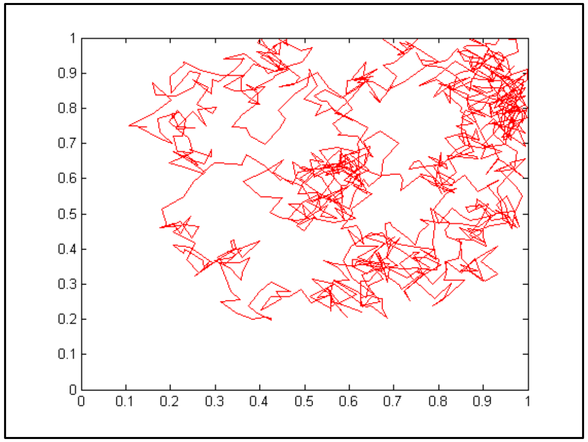
Aimone, Deng and Gage
Neuron; 2011

- Dentate Gyrus performs sparse coding for episodic memories
- Mature neurons are tightly tuned to specific features
  - *Not all events will activate mature neurons*
- Immature neurons are broadly tuned
  - *All events will activate some immature neurons*
- Neurons mature to be specialized to those events later
  - *Coding range of network gets more sophisticated over time*

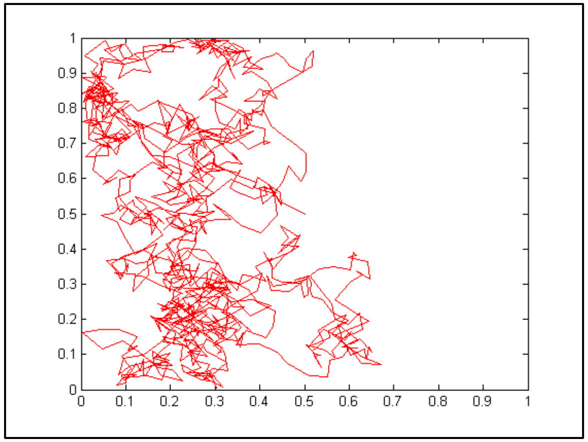
Computational Paradigm



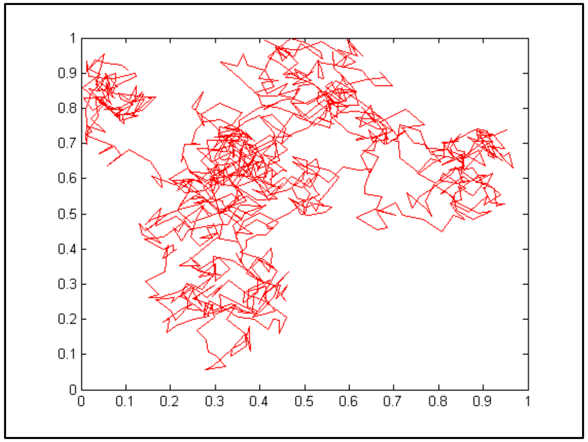
Sample Paths



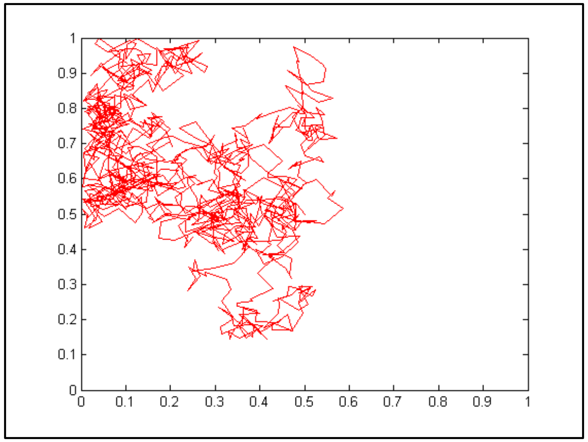
Random Path 1



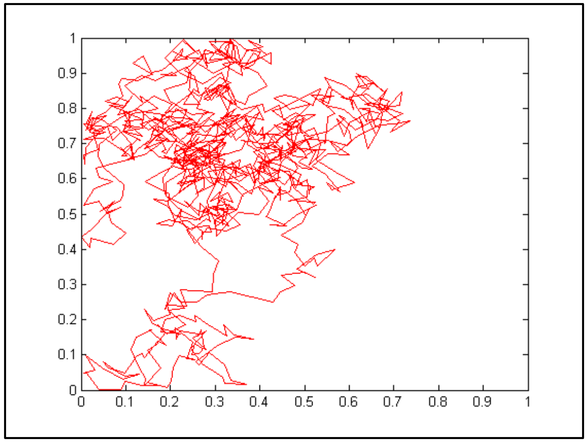
Random Path 2



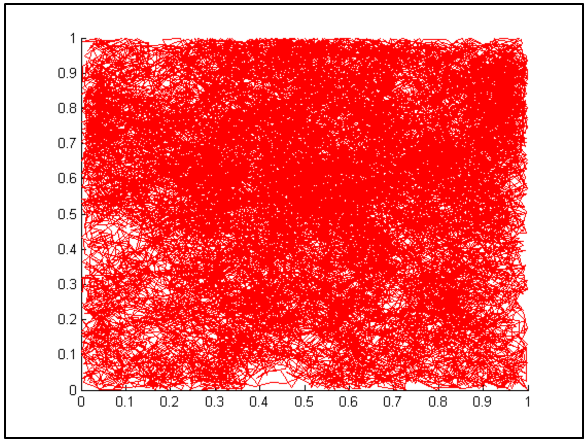
Random Path 3



Random Path 4

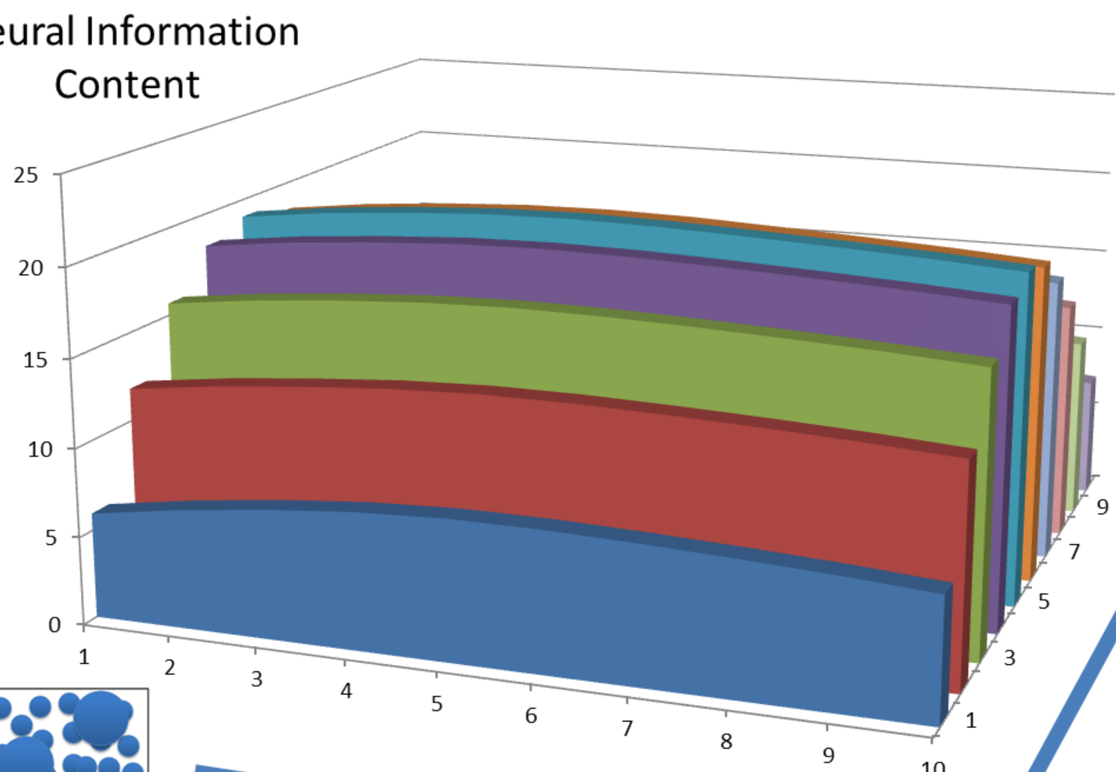


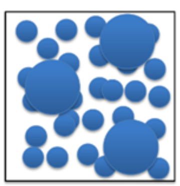
Random Path 5

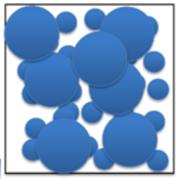


Combined Random Path Coverage

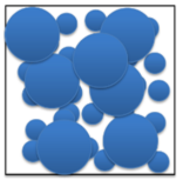
Results Exploring Mix Ratio

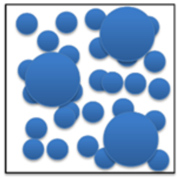






More young neurons
(i.e. Increased
neurogenesis)





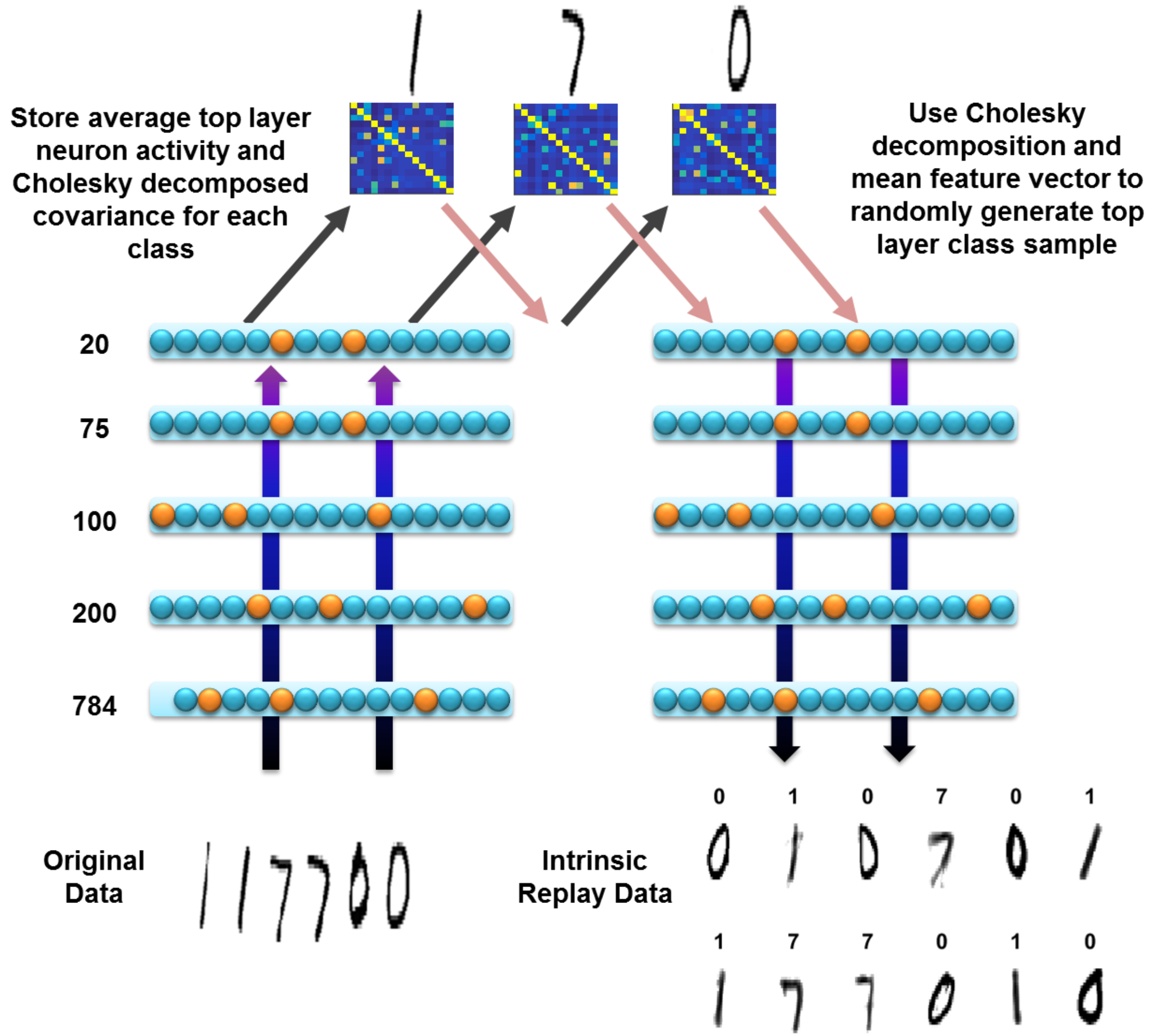
More young neurons
(i.e. Increased
neurogenesis)

100 Neurons
10% Mix Ratio

Implications for Computation

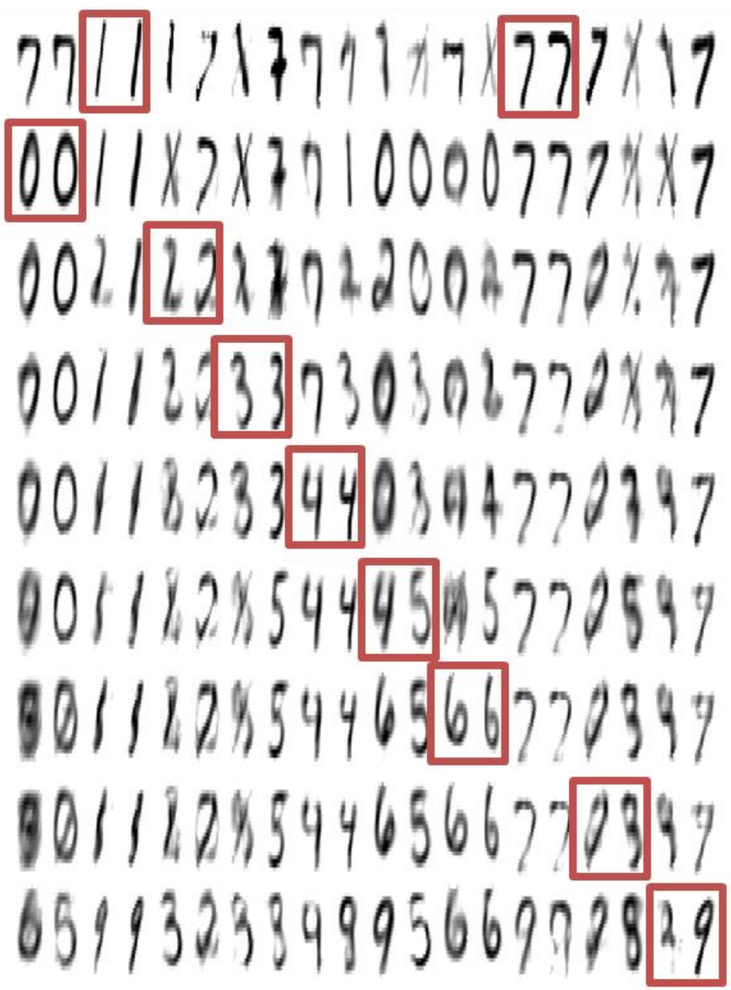
- Neurogenic Deep Learning
- High Performance Computing
- Hippocampal Models
  - Modulation Model
  - SVM Model

Neurogenic Deep Learning

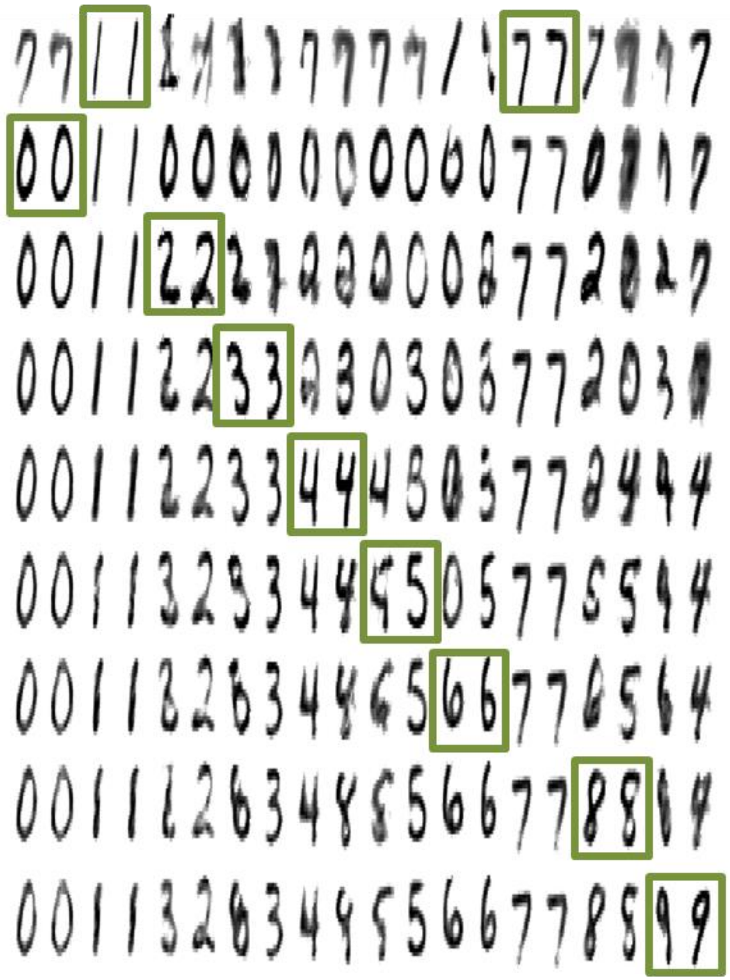


Draelos et al. Deep Learning for Transfer Learning and Concept Drift through Adult Neurogenesis-inspired Adaptation (in preparation)

Neurogenic Deep Learning



Without neurogenesis



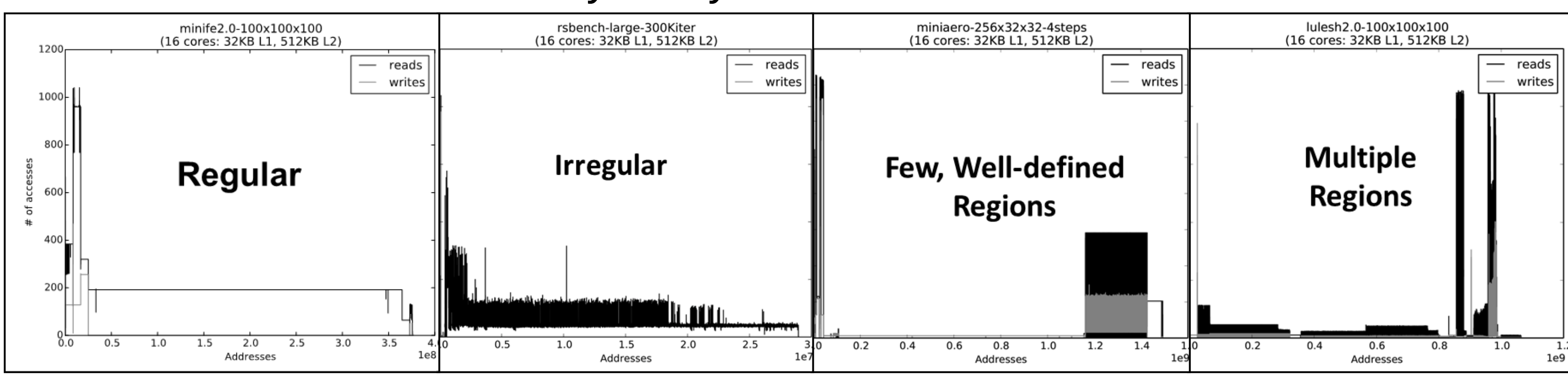
With neurogenesis

High Performance Computing

Exascale-class supercomputers will require unprecedented amounts of memory bandwidth and capacity - To satisfy these requirements, vendors are proposing Multi-Level Memory (MLM) combining different memory technologies in a single system

Proposing to explore the ability of neural inspired dynamic memory management strategies to learn application specific memory management schemes for HPC architectures

Memory Analysis: Diverse Patterns

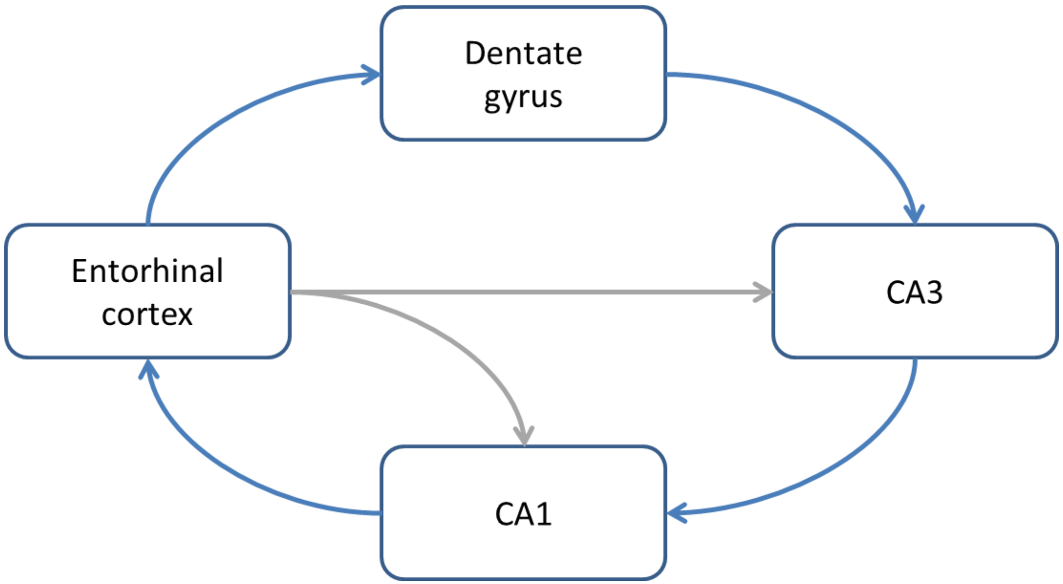


Physical Memory Address Histograms

Hippocampus Modeling

- Proposed to enhance the encoding of new memories by performing pattern separation
- Orthogonalization

- Primary input to the hippocampal formation
- Grid cell encoding



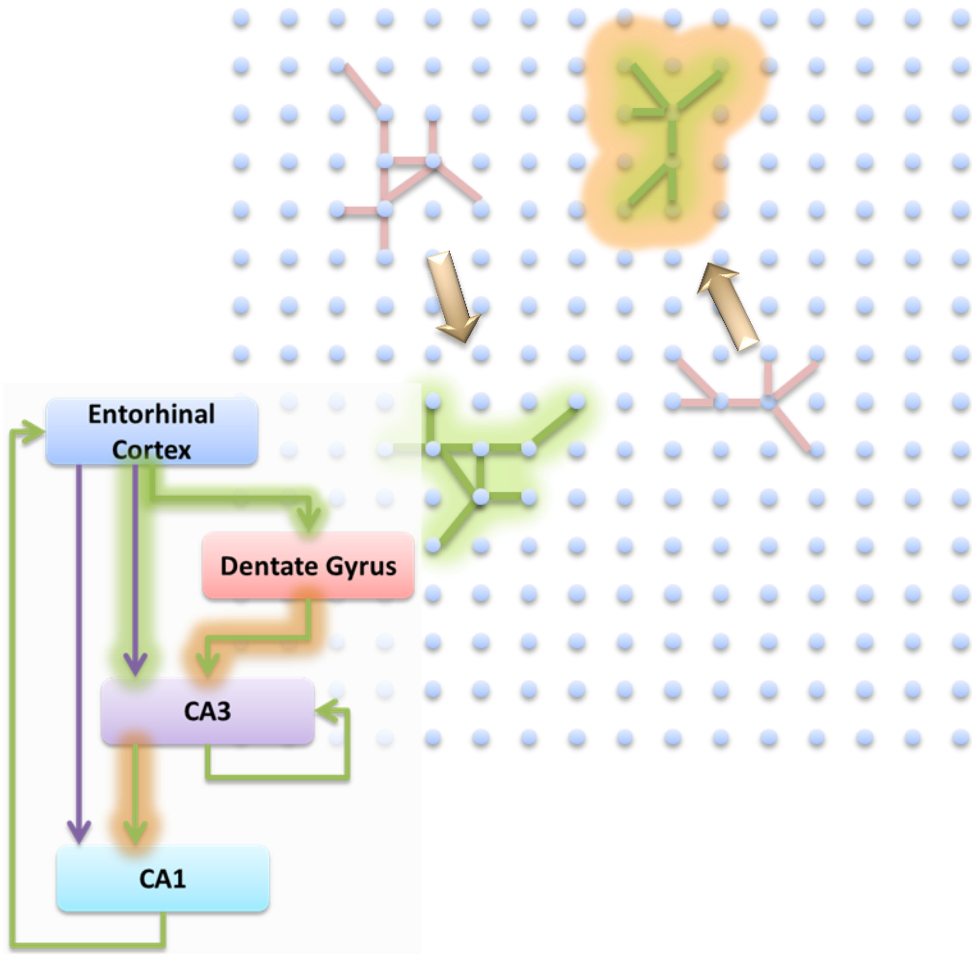
- Autoassociative encoding of input patterns
- Pattern completion

- Comparator of the input from EC with the output from CA3

*Scholarpedia Function of Hippocampal subregions

A New Modulation Model

- CA3 is static dynamical “soup”
- EC->CA3 selects population of stable attractor paths (green) that are valid for a given context
- EC->DG induces a sparse and *unique* representation of EC in DG
- DG->CA3 activates some ensemble (~uniquely) in CA3, which settles into one of the valid attractors
- EC->CA1 connections learns that this attractor (set of CA3 representations) is associated with some EC representation
  - CA1 “learns” to read CA3 attractors
  - Context dependent readout
- In future, partial EC input can reactivate CA1 accordingly



Alternative Hippocampus Perspective

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Is there a support vector machine hiding in the dentate gyrus?

John L. Baker

School of Computational Sciences, George Mason University, 4400 University Drive, Fairfax, VA 22030, USA

Abstract

The dentate gyrus has physiological and related behavioral properties suggesting that it implements functions within the hippocampus partially associated with sensory pattern recognition. A top-down dentate gyrus model is defined in terms of an idealized support vector machine pattern recognizer constructed from spiking neurons. The resulting construction offers parallels with dentate gyrus morphology and offers explanation of some of its unique properties, in particular, the mossy fiber pathway and its connection with CA3 pyramidal cells. Derived learning rules suggest properties of the mossy fibers that might be tested experimentally.

Keywords: Hippocampus; Dentate gyrus; Mossy fiber; Support vector machine; Pattern recognition

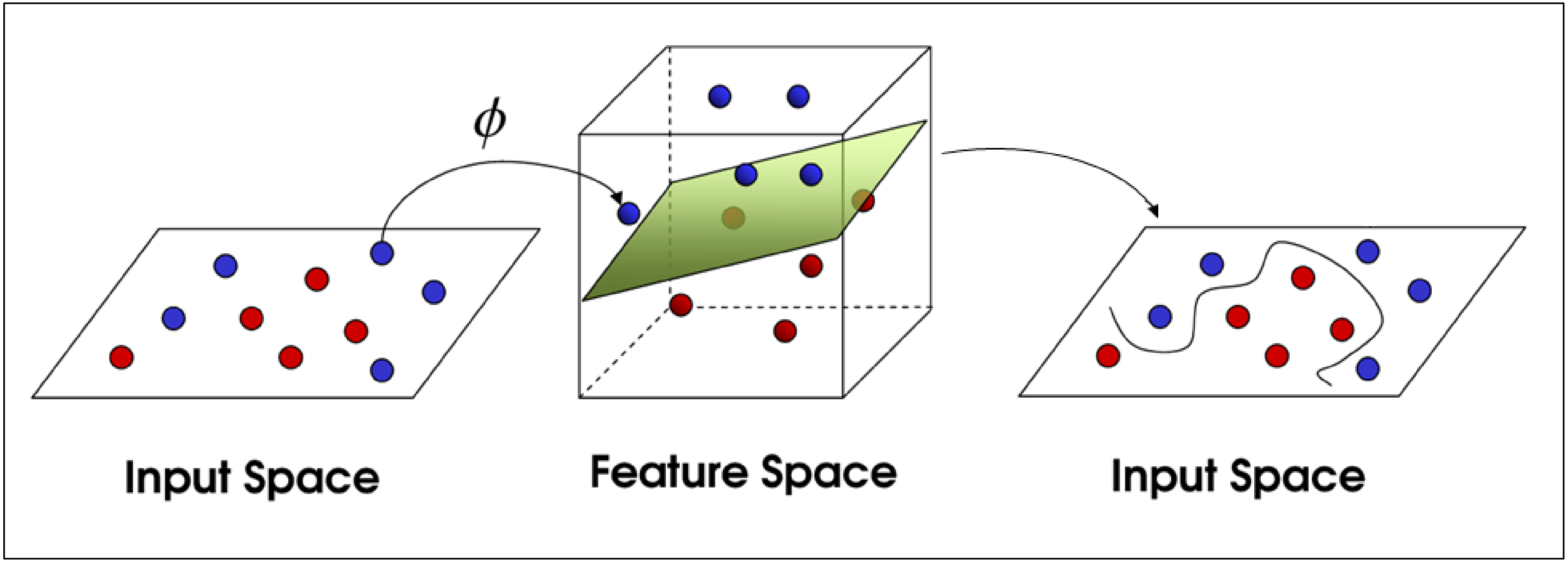
SVM Hippocampus Perspective

- "Is there a support vector machine hiding in the dentate gyrus?"
  - John L. Baker - Neurocomputing 2003

- Our conjecture – rather there is a support vector machine hiding in the hippocampus (EC – DG – CA3)

SVM Hippocampus Perspective

We hypothesize that the role of the hippocampus in information processing is …



to restructure and refine the multimodal associative encoding provided by the entorhinal cortex (EC)

through a high dimensional adaptive transformation in dentate gyrus (DG)

and subsequent compressive encoding by the CA3

SVM Hippocampus Perspective

- Implications -
- However, unlike conventional SVM theory, the existence of adult neurogenesis in DG confers an adaptive high dimensional projection which impacts the resulting CA3 encoding (or discriminant in a canonical SVM)
- VC dimension (which SVM is based upon) describes the ability of a set of functions to separate data in a space

Summary

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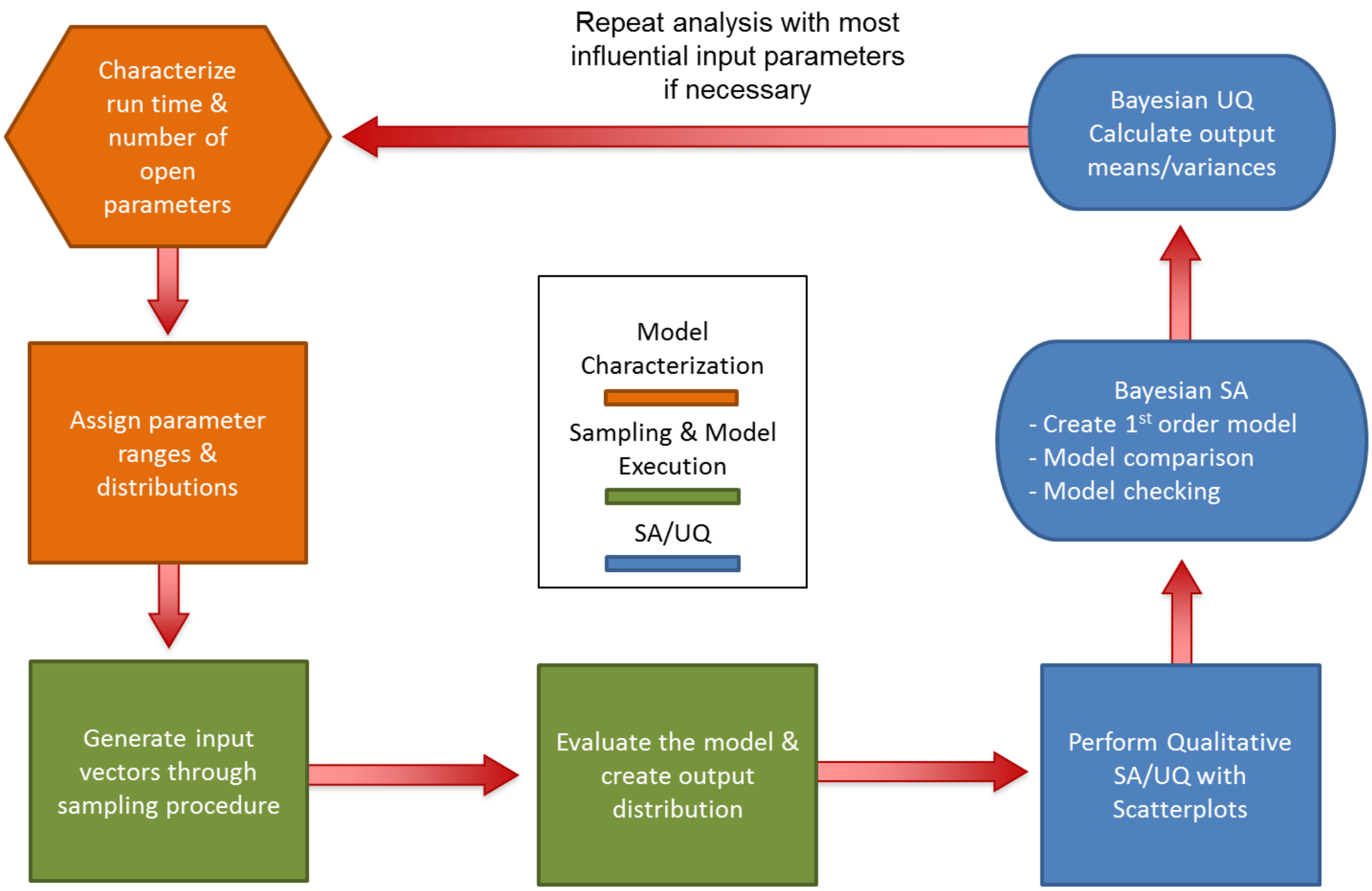
- Presented a metric & computational paradigm for quantifying neural information content
  - As a specific case study we have used this framework to study the impact of hippocampal neurogenesis
  - Experimentally shown benefit to mixed coding
  - Quantifying Neural Information Content: A Case Study of the Impact of Hippocampal Adult Neurogenesis (IJCNN 2016 submission)

- Several exciting implications for computation
  - Computer design (conventional and neuromorphic)
  - New perspectives on hippocampal function in information encoding & transformation (potential implications for machine learning and insights for neural computation)

Backup

UQ & SA

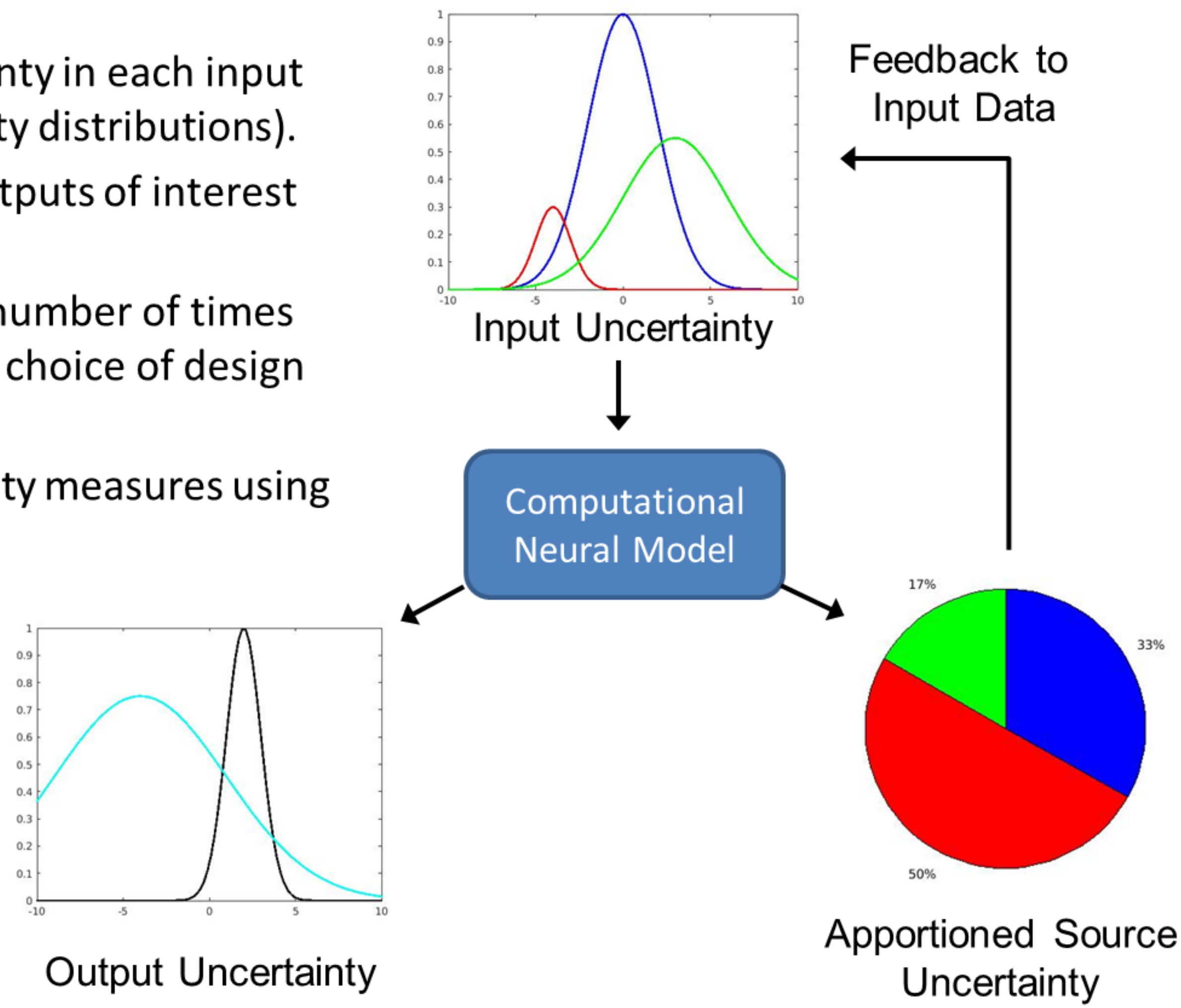


Repeat analysis with most influential input parameters if necessary
Characterize run time & number of open parameters
Bayesian UQ Calculate output means/variances
Model Characterization
Sampling & Model Execution
SA/UQ
Assign parameter ranges & distributions
Bayesian SA
- Create 1st order model
- Model comparison
- Model checking
Generate input vectors through sampling procedure
Evaluate the model & create output distribution
Perform Qualitative SA/UQ with Scatterplots

UQ & SA

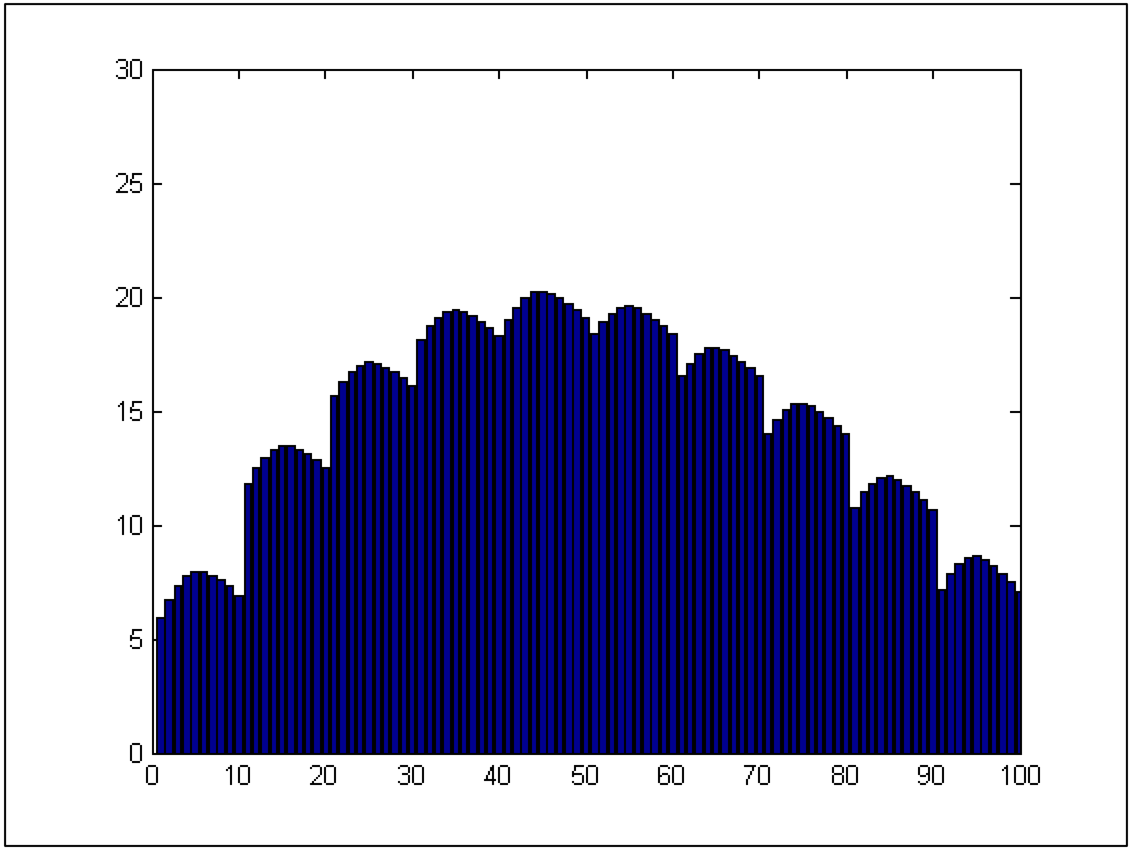
Core SA methodology:

1. Estimate uncertainty in each input (ranges, probability distributions).
2. Identify model outputs of interest to be analyzed.
3. Run the model a number of times using appropriate choice of design of experiments .
4. Calculate sensitivity measures using model outputs.



Exploring Mix Ratio – 100 Neurons

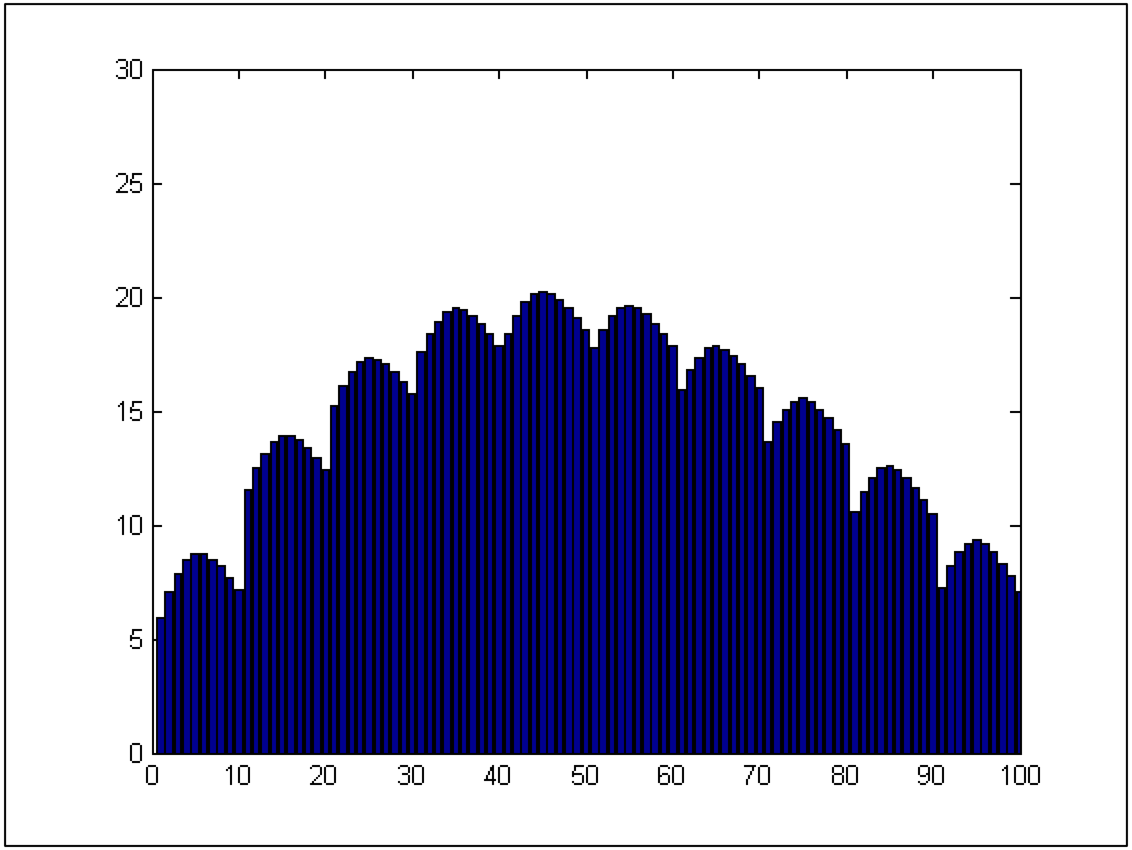
Normalized Information Content



10% Mix Ratio

Exploring Mix Ratio – 100 Neurons

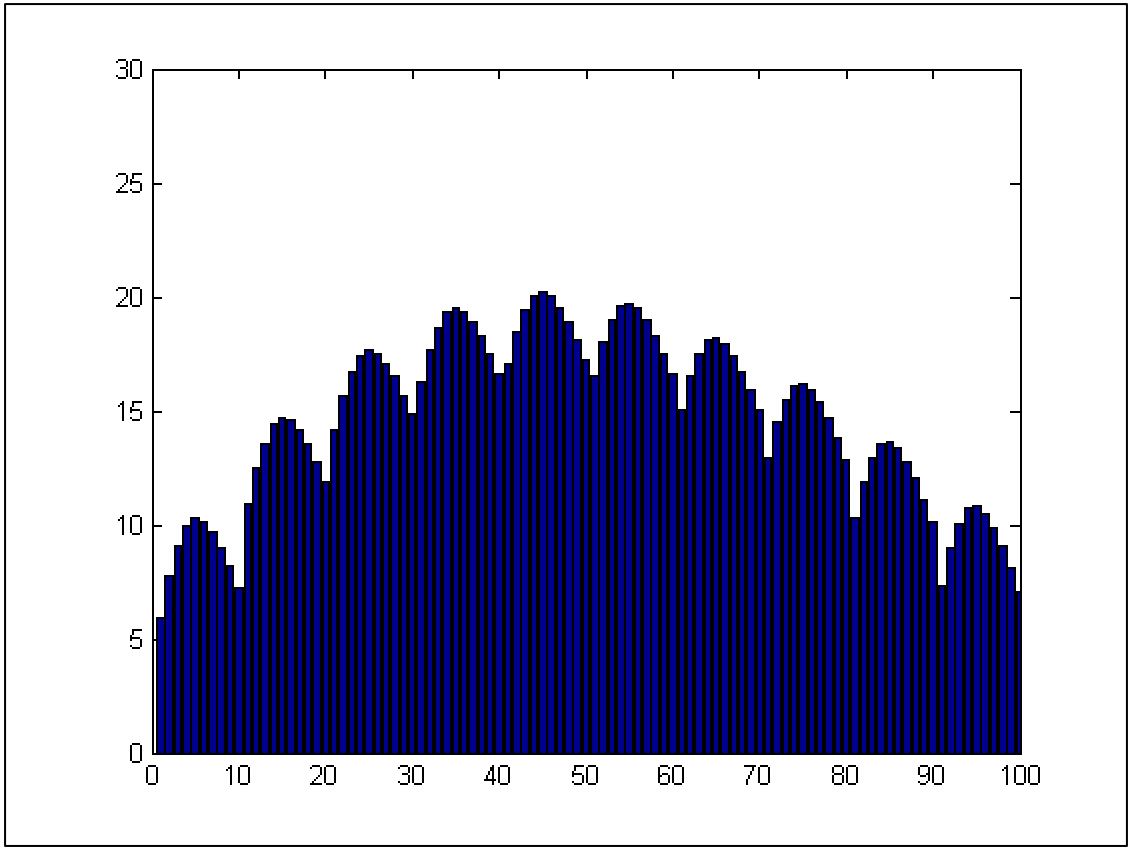
Normalized Information Content



15% Mix Ratio

Exploring Mix Ratio – 100 Neurons

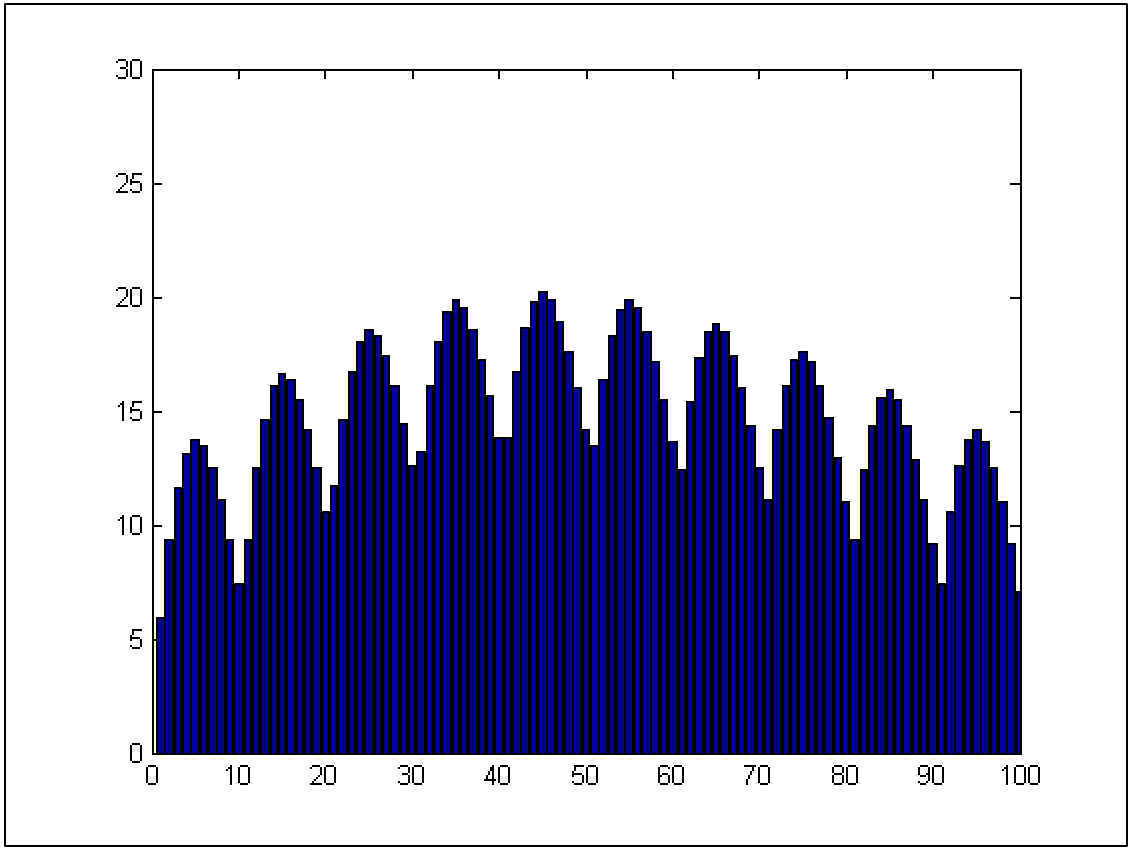
Normalized
Information
Content



25% Mix Ratio

Exploring Mix Ratio – 100 Neurons

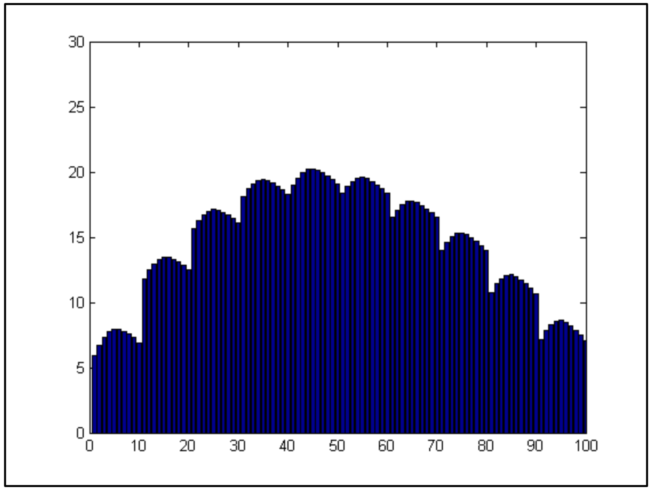
Normalized Information Content



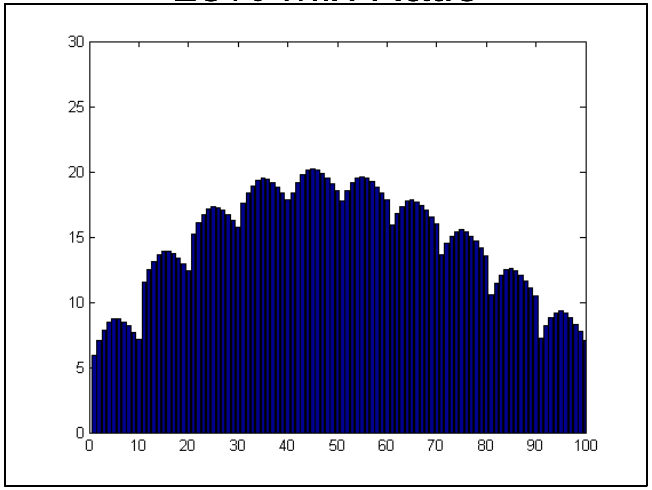
50% Mix Ratio

Exploring Mix Ratio – 100 Neurons

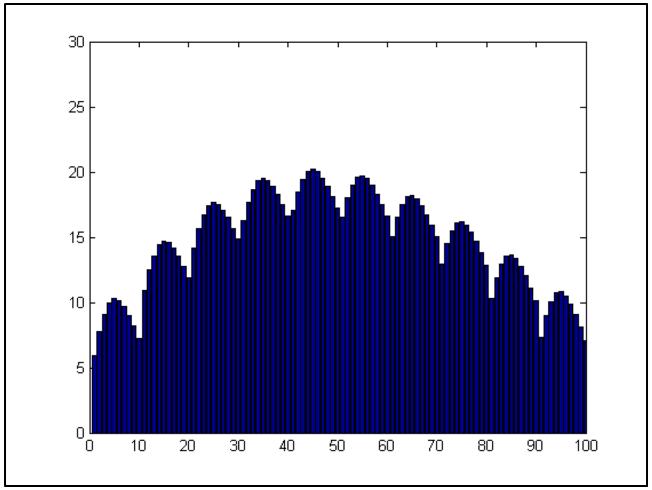
10% Mix Ratio



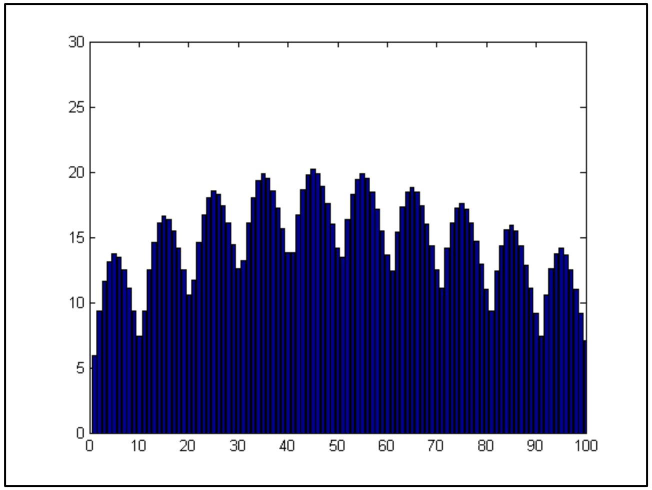
15% Mix Ratio



25% Mix Ratio



50% Mix Ratio



Mixed Coding Analysis

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10 % Mix Ratio – 100 Neurons Resolution 25

	0.0100	0.0233	0.0367	0.0500	0.0633	0.0767	0.0900	0.1033	0.1167	0.1300
0.0100	5.9559	6.7196	7.3064	7.7418	7.9513	7.9348	7.7806	7.5582	7.2862	6.9229
0.0233	11.8376	12.4588	12.9120	13.2711	13.4474	13.4236	13.2805	13.0811	12.8301	12.4988
0.0367	15.6965	16.2832	16.6958	16.9875	17.1077	17.0479	16.8820	16.6673	16.4103	16.0795
0.0500	18.1140	18.6909	19.0770	19.3526	19.4350	19.3490	19.1633	18.9282	18.6609	18.3250
0.0633	18.9772	19.5544	19.9337	20.1879	**20.2609**	20.1569	19.9554	19.7095	19.4361	19.0946
0.0767	18.3350	18.9188	19.2982	19.5461	19.6036	19.5014	19.2722	19.0193	18.7362	18.3870
0.0900	16.4977	17.0915	17.4734	17.7200	17.7725	17.6462	17.4234	17.1551	16.8637	16.5047
0.1033	14.0290	14.6394	15.0306	15.2815	15.3323	15.1964	14.9572	14.6821	14.3740	14.0053
0.1167	10.7681	11.4036	11.8135	12.0679	12.1104	11.9657	11.7076	11.4127	11.0858	10.6980
0.1300	7.1748	7.8600	8.2914	8.5696	8.6149	8.4560	8.1820	7.8634	7.5114	7.0811

Mixed Coding Analysis

15 % Mix Ratio – 100 Neurons Resolution 25

	0.0100	0.0233	0.0367	0.0500	0.0633	0.0767	0.0900	0.1033	0.1167	0.1300
0.0100	5.9559	7.0405	7.8437	8.4354	8.7266	8.7121	8.5028	8.1691	7.6834	7.1075
0.0233	11.5624	12.4588	13.1157	13.6348	13.8950	13.8826	13.6917	13.3867	12.9394	12.4123
0.0367	15.2479	16.0969	16.6958	17.1337	17.3307	17.2776	17.0668	16.7514	16.3050	15.7859
0.0500	17.5447	18.3829	18.9417	19.3526	19.5034	19.4160	19.1822	18.8454	18.3873	17.8680
0.0633	18.3570	19.1935	19.7425	20.1241	**20.2609**	20.1490	19.8968	19.5443	19.0741	18.5448
0.0767	17.7287	18.5722	19.1230	19.4951	19.6106	19.5014	19.2153	18.8484	18.3635	17.8239
0.0900	15.9521	16.8108	17.3668	17.7378	17.8420	17.7046	17.4234	17.0334	16.5403	15.9857
0.1033	13.5976	14.4818	15.0489	15.4271	15.5339	15.3840	15.0801	14.6821	14.1591	13.5857
0.1167	10.5665	11.4831	12.0751	12.4585	12.5544	12.3917	12.0633	11.6353	11.0858	10.4849
0.1300	7.1940	8.1769	8.7977	9.2045	9.3068	9.1294	8.7861	8.3323	7.7434	7.0811

Mixed Coding Analysis

25 % Mix Ratio – 100 Neurons Resolution 25

	0.0100	0.0233	0.0367	0.0500	0.0633	0.0767	0.0900	0.1033	0.1167	0.1300
0.0100	5.9559	7.7698	9.0473	9.9208	10.2719	10.1307	9.6809	9.0324	8.1598	7.2303
0.0233	10.9018	12.4588	13.5763	14.3866	14.7260	14.5934	14.1789	13.5779	12.7617	11.9020
0.0367	14.1832	15.6624	16.6958	17.4008	17.6734	17.5199	17.0895	16.4918	15.6912	14.8495
0.0500	16.2576	17.7151	18.6841	19.3526	19.5609	19.3625	18.9131	18.2983	17.4895	16.6558
0.0633	17.0444	18.5023	19.4561	20.0741	**20.2609**	20.0302	19.5528	18.9201	18.0997	17.2571
0.0767	16.5544	18.0202	18.9771	19.5768	19.7358	19.5014	18.9833	18.3260	17.4857	16.6299
0.0900	15.0314	16.5195	17.4778	18.0804	18.2181	17.9394	17.4234	16.7388	15.8836	15.0118
0.1033	12.9730	14.5038	15.4772	16.0816	16.2200	15.9287	15.3802	14.6821	13.7847	12.8802
0.1167	10.3447	11.9269	12.9329	13.5492	13.6722	13.3577	12.7720	12.0246	11.0858	10.1448
0.1300	7.3598	9.0347	10.0787	10.7117	10.8336	10.4962	9.8848	9.1019	8.1075	7.0811

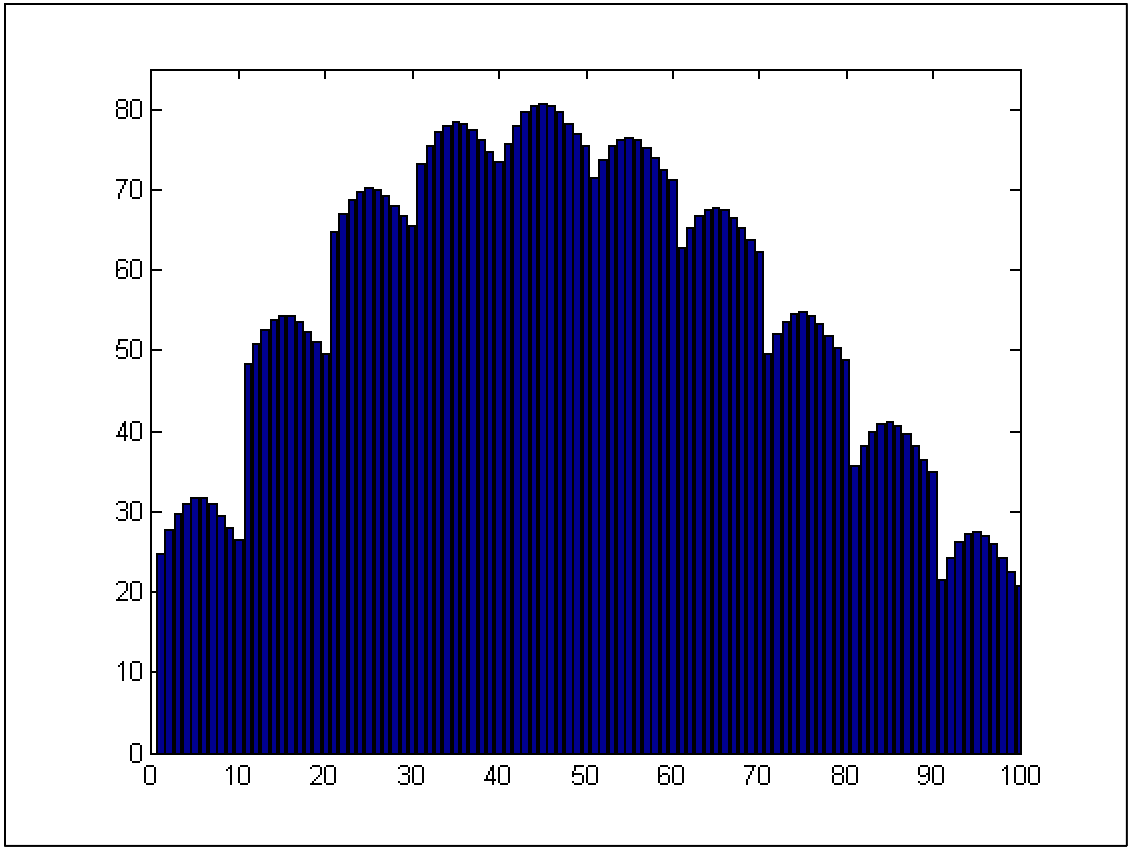
Mixed Coding Analysis

50 % Mix Ratio – 100 Neurons Resolution 25

	0.0100	0.0233	0.0367	0.0500	0.0633	0.0767	0.0900	0.1033	0.1167	0.1300
0.0100	5.9559	9.3569	11.6592	13.1418	13.7382	13.4539	12.4842	11.1033	9.3595	7.3925
0.0233	9.3748	12.4588	14.6276	16.0676	16.6640	16.3889	15.4599	14.1340	12.4632	10.6018
0.0367	11.6915	14.6370	16.6958	18.0350	18.5846	18.3056	17.3790	16.0719	14.4299	12.6118
0.0500	13.2043	16.1116	18.0655	19.3526	19.8269	19.5149	18.5760	17.2657	15.6292	13.8334
0.0633	13.7856	16.6910	18.5976	19.8101	**20.2609**	19.9005	18.9433	17.6122	15.9676	14.1755
0.0767	13.4536	16.3713	18.2781	19.4541	19.8585	19.5014	18.4797	17.1280	15.4765	13.6671
0.0900	12.4401	15.3982	17.3068	18.4766	18.8544	18.4420	17.4234	16.0286	14.3491	12.4920
0.1033	11.1219	14.1357	16.0594	17.2220	17.5854	17.1463	16.0959	14.6821	12.9349	11.0349
0.1167	9.3309	12.4169	14.3747	15.5425	15.8929	15.4468	14.3649	12.8854	11.0858	9.1248
0.1300	7.3960	10.5853	12.5822	13.7701	14.1261	13.6693	12.5408	11.0121	9.1565	7.0811

Exploring Mix Ratio – 484 Neurons

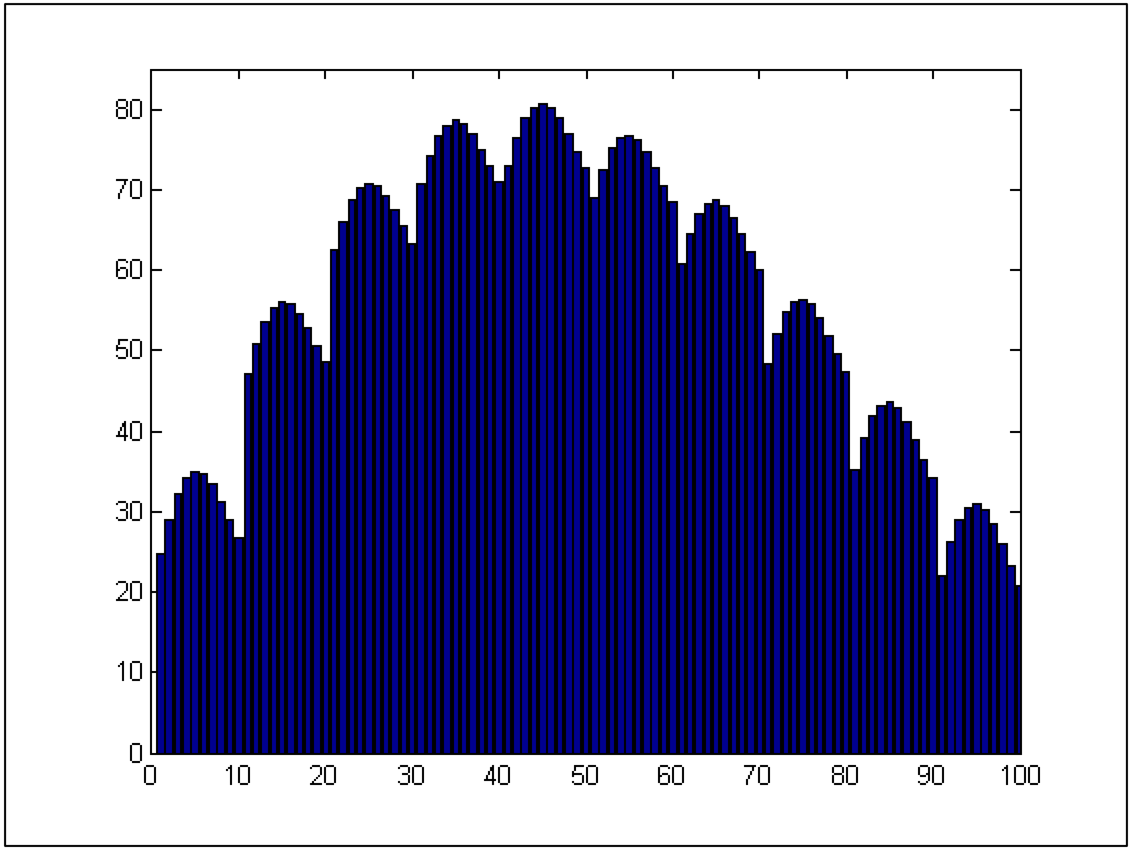
Normalized Information Content



10% Mix Ratio

Exploring Mix Ratio – 484 Neurons

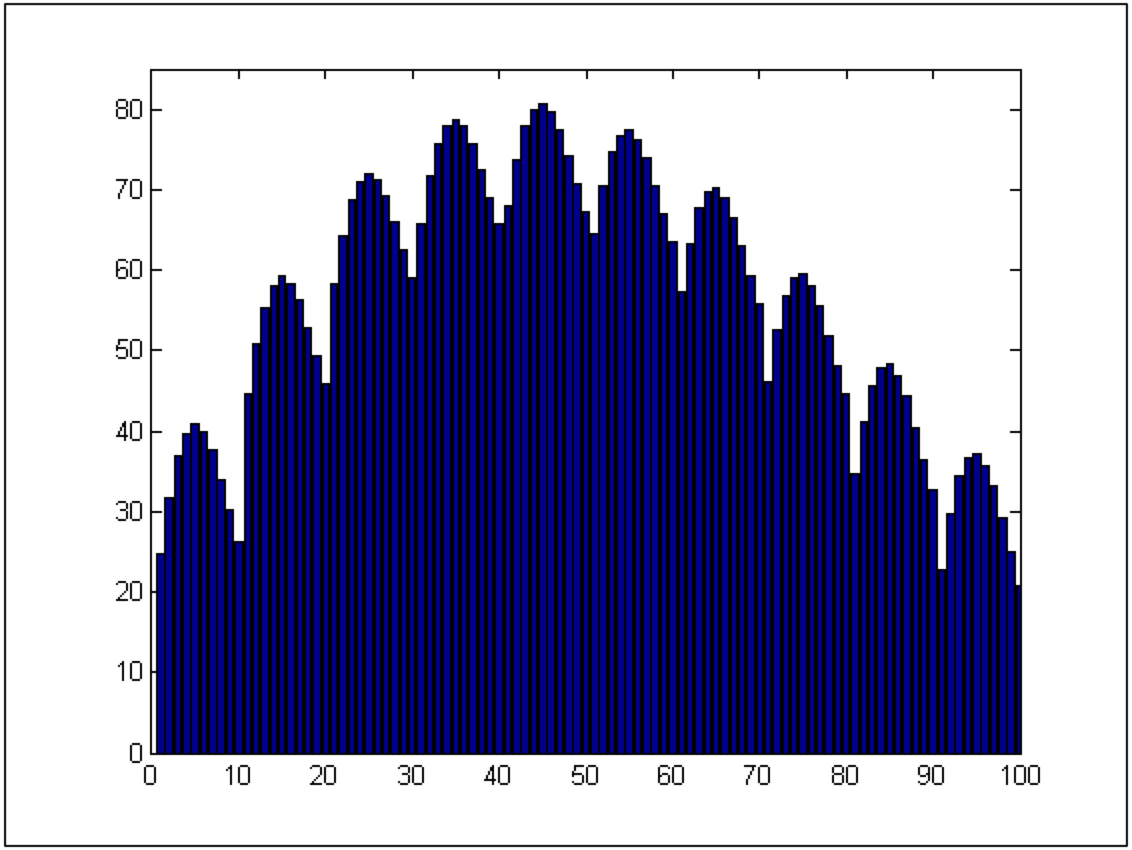
Normalized Information Content



15% Mix Ratio

Exploring Mix Ratio – 484 Neurons

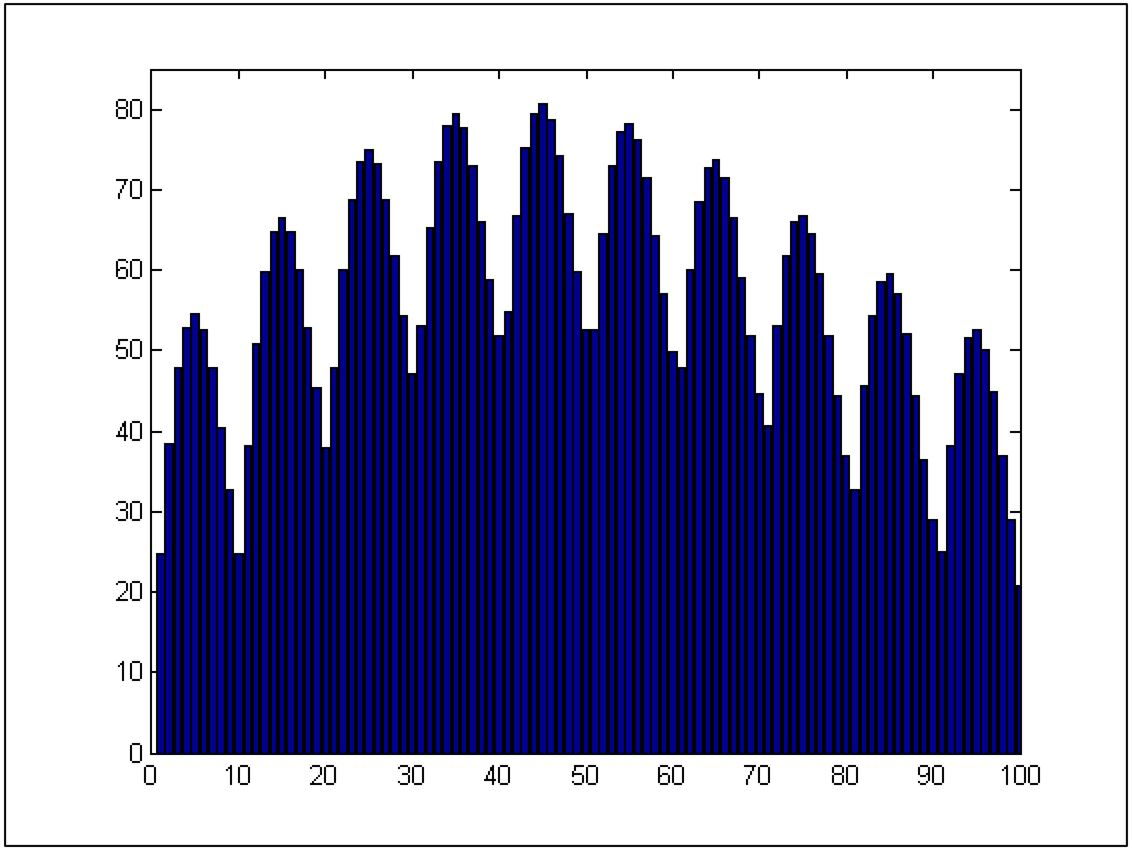
Normalized Information Content



25% Mix Ratio

Exploring Mix Ratio – 484 Neurons

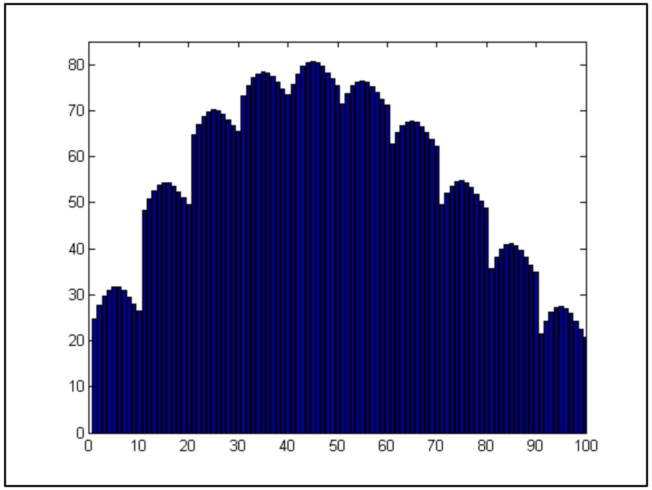
Normalized Information Content



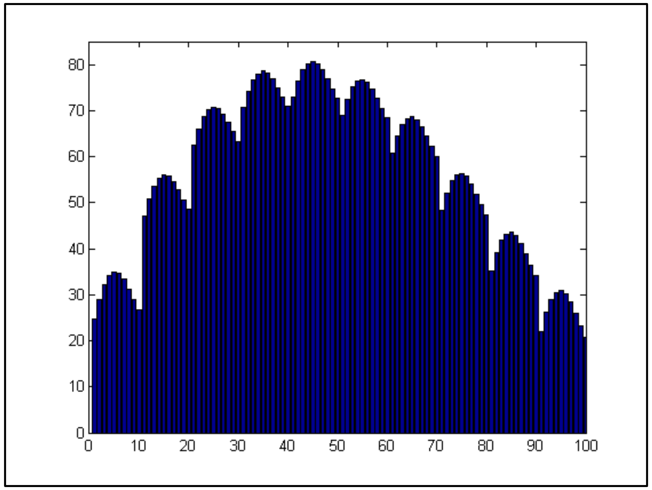
50% Mix Ratio

Exploring Mix Ratio – 484 Neurons

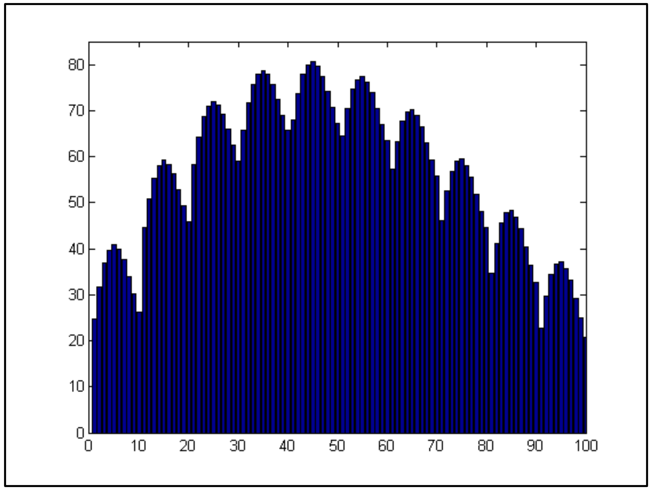
10% Mix Ratio



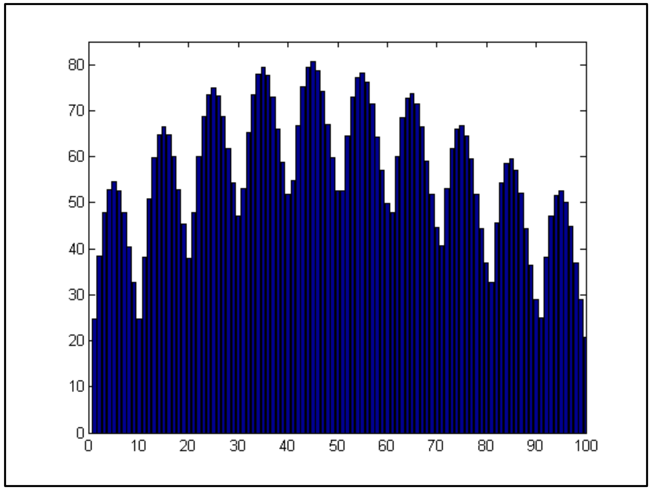
15% Mix Ratio



25% Mix Ratio



50% Mix Ratio



Mixed Coding Analysis

10 % Mix Ratio – 484 Neurons Resolution 25

	0.0100	0.0233	0.0367	0.0500	0.0633	0.0767	0.0900	0.1033	0.1167	0.1300
0.0100	24.7271	27.5937	29.7587	31.0333	31.7189	31.6527	30.8426	29.5087	27.9684	26.4899
0.0233	48.3157	50.7268	52.5678	53.6935	54.3415	54.3270	53.5904	52.3700	50.9840	49.6600
0.0367	64.7123	66.9991	68.6563	69.6074	70.1204	70.0169	69.2703	68.0573	66.7081	65.4250
0.0500	73.2885	75.5451	77.1568	78.0082	78.3925	78.2533	77.4089	76.1769	74.7966	73.5111
0.0633	75.6715	77.9349	79.5517	80.3302	**80.6391**	80.4136	79.5419	78.2619	76.8588	75.5541
0.0767	71.4474	73.7647	75.3589	76.1539	76.4361	76.1251	75.2072	73.8830	72.4352	71.1277
0.0900	62.7983	65.1495	66.7879	67.5760	67.8494	67.5068	66.5221	65.1179	63.6374	62.2980
0.1033	49.5488	51.9744	53.6736	54.5051	54.7700	54.3910	53.3588	51.8963	50.3627	48.9569
0.1167	35.6726	38.2225	39.9848	40.8447	41.1327	40.7357	39.6699	38.1379	36.5082	35.0128
0.1300	21.5755	24.3206	26.2018	27.1111	27.4294	27.0303	25.8869	24.2483	22.4821	20.8459

Mixed Coding Analysis

Sandia National Laboratories

15 % Mix Ratio – 484 Neurons Resolution 25

	0.0100	0.0233	0.0367	0.0500	0.0633	0.0767	0.0900	0.1033	0.1167	0.1300
0.0100	24.7271	28.9997	32.2323	34.0773	34.9177	34.6139	33.3283	31.2064	28.9312	26.5974
0.0233	47.0641	50.7268	53.5728	55.2817	56.1030	55.8571	54.6686	52.7286	50.6245	48.5331
0.0367	62.5691	66.0854	68.6563	70.1201	70.8087	70.5242	69.3409	67.4437	65.4304	63.3541
0.0500	70.7100	74.1744	76.6526	78.0082	78.5459	78.1698	76.9137	74.9837	72.9135	70.8730
0.0633	72.9808	76.4623	78.9623	80.2117	**80.6391**	80.1687	78.8497	76.8711	74.8011	72.7438
0.0767	69.0276	72.5547	75.0693	76.3061	76.6930	76.1251	74.7295	72.6969	70.5713	68.4836
0.0900	60.8861	64.4590	67.0105	68.2765	68.6041	67.9980	66.5221	64.3733	62.2082	60.0791
0.1033	48.3618	52.0545	54.6975	56.0036	56.3568	55.6866	54.1214	51.8963	49.6086	47.4228
0.1167	35.2164	39.0819	41.8100	43.1574	43.5407	42.8409	41.2489	38.9037	36.5082	34.1875
0.1300	21.9605	26.0982	29.0031	30.4049	30.8247	30.1114	28.4301	25.9556	23.3576	20.8459

Mixed Coding Analysis

25 % Mix Ratio – 484 Neurons Resolution 25

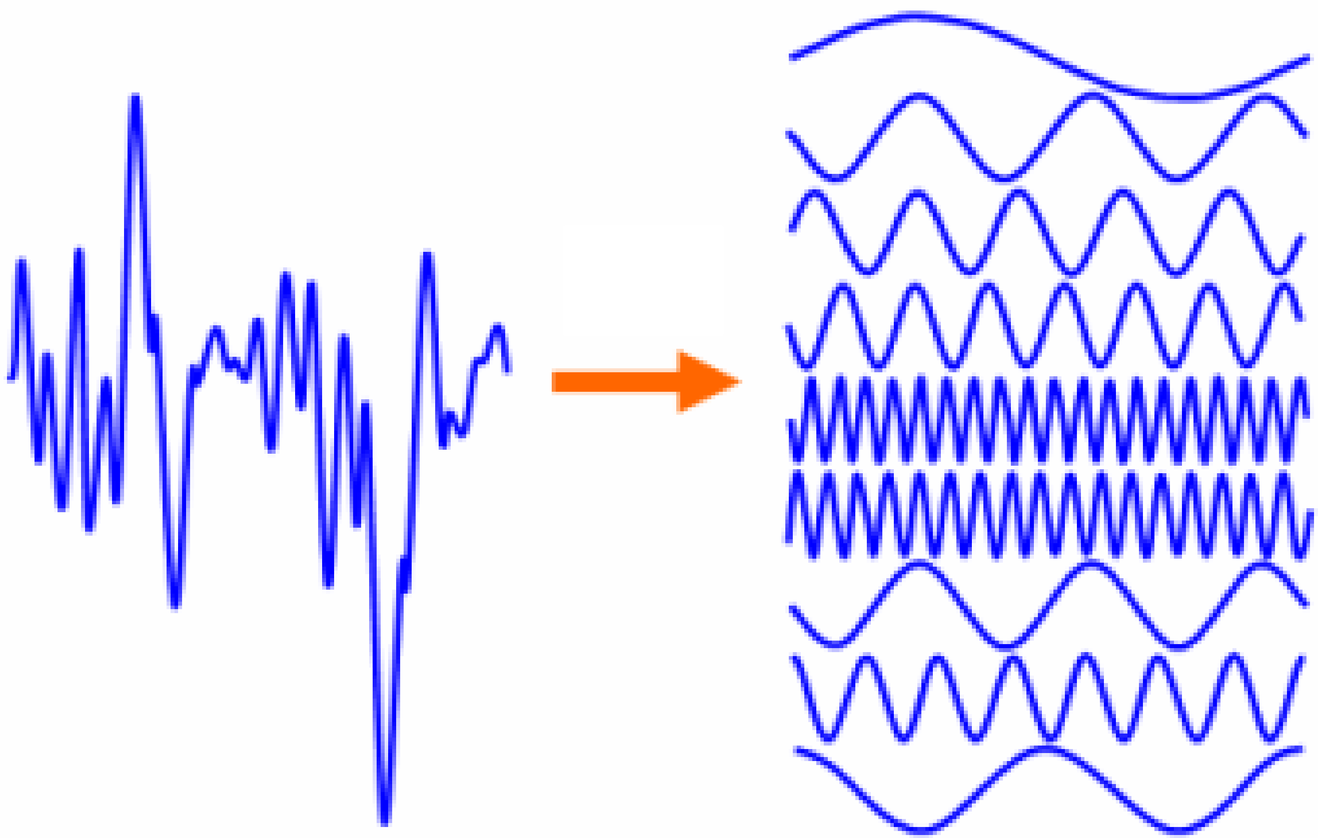
	0.0100	0.0233	0.0367	0.0500	0.0633	0.0767	0.0900	0.1033	0.1167	0.1300
0.0100	24.7271	31.7368	36.8724	39.6893	40.7778	39.8264	37.6824	34.0280	30.1728	26.3339
0.0233	44.5368	50.7268	55.4128	58.1081	59.1653	58.3251	56.3376	52.9223	49.3141	45.7866
0.0367	58.3806	64.3237	68.6563	71.0742	72.0338	71.1912	69.2337	65.8989	62.4102	58.9891
0.0500	65.6900	71.5939	75.7466	78.0082	78.7825	77.8214	75.7843	72.4592	68.9889	65.6344
0.0633	67.8657	73.7479	77.9029	80.0036	**80.6391**	79.5576	77.4699	74.1249	70.5982	67.2348
0.0767	64.5709	70.5259	74.7240	76.7942	77.3056	76.1251	73.9062	70.4589	66.8698	63.4313
0.0900	57.2889	63.3275	67.6050	69.6968	70.1507	68.8452	66.5221	62.9234	59.2795	55.7790
0.1033	46.2110	52.4426	56.7977	58.9415	59.4100	58.0482	55.6050	51.8963	48.1042	44.5011
0.1167	34.5898	41.0636	45.5762	47.7907	48.2760	46.8449	44.3474	40.4721	36.5082	32.7380
0.1300	22.8459	29.7092	34.4010	36.6907	37.2158	35.7634	33.1822	29.1253	24.8989	20.8459

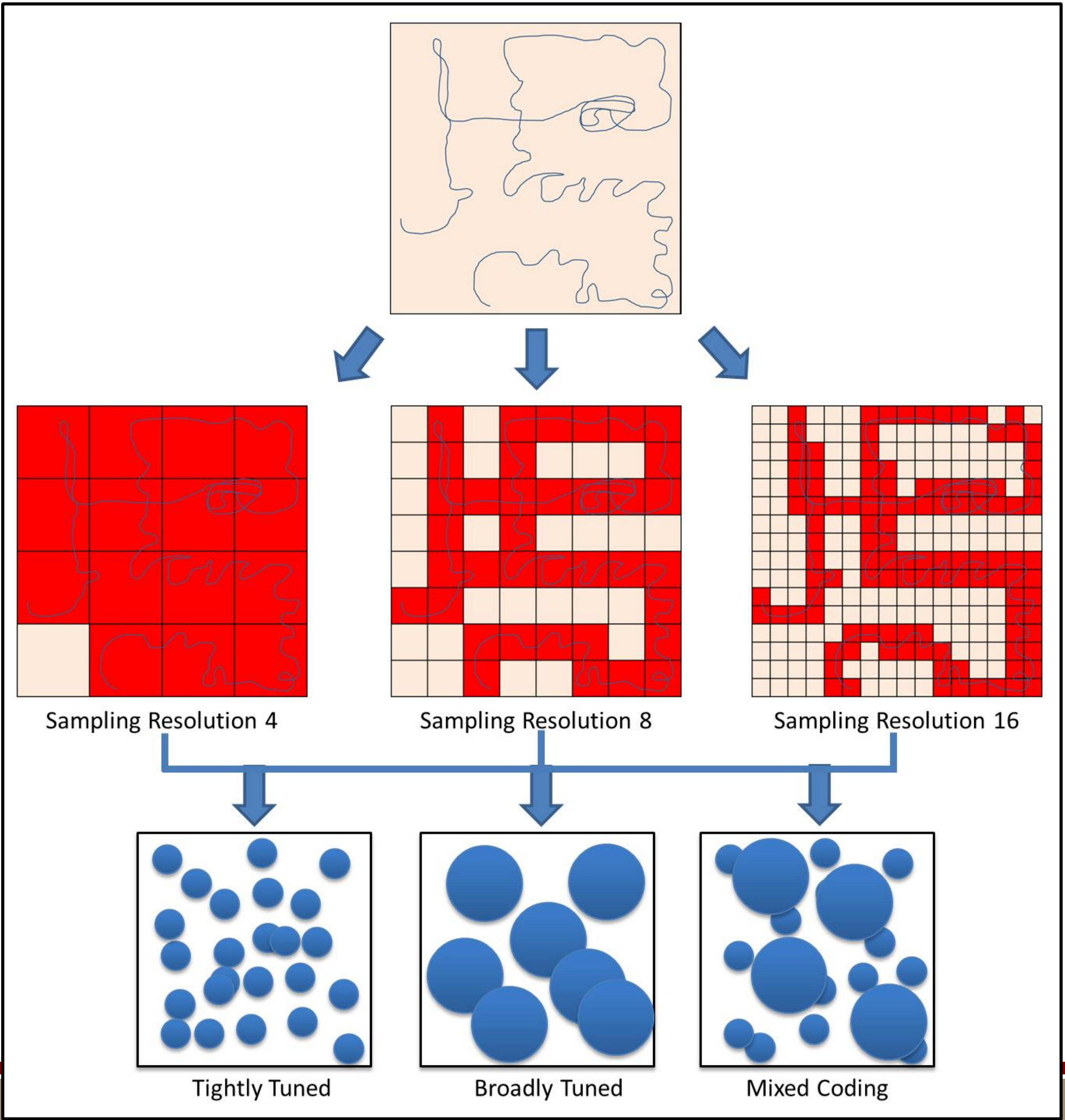
Mixed Coding Analysis

50 % Mix Ratio – 484 Neurons Resolution 25

	0.0100	0.0233	0.0367	0.0500	0.0633	0.0767	0.0900	0.1033	0.1167	0.1300
0.0100	24.7271	38.2994	47.7917	52.8375	54.4835	52.6209	47.8873	40.4250	32.6637	24.7732
0.0233	38.1765	50.7268	59.8372	64.7800	66.4139	64.6544	60.0689	52.8868	45.4372	38.0028
0.0367	47.8492	59.9897	68.6563	73.3382	74.9612	73.1872	68.6782	61.6530	54.3595	47.1195
0.0500	53.0875	65.1212	73.5132	78.0082	79.3990	77.5691	73.0615	66.0600	58.8500	51.6989
0.0633	54.7567	66.7937	75.1582	79.3962	**80.6391**	78.6529	74.0863	67.0115	59.7912	52.6670
0.0767	52.4883	64.5940	72.9910	77.1642	78.2280	76.1251	71.3851	64.2156	56.9161	49.7470
0.0900	47.7477	60.0371	68.4981	72.6650	73.6748	71.3666	66.5221	59.1518	51.7985	44.5547
0.1033	40.5609	53.1048	61.7064	65.8989	66.8411	64.4409	59.4113	51.8963	44.3298	36.9263
0.1167	32.7405	45.6124	54.3573	58.6392	59.5748	57.1225	52.0016	44.2844	36.5082	28.8386
0.1300	24.9114	38.2521	47.1817	51.5281	52.5034	50.0495	44.8227	36.9468	28.8824	20.8459

Transform





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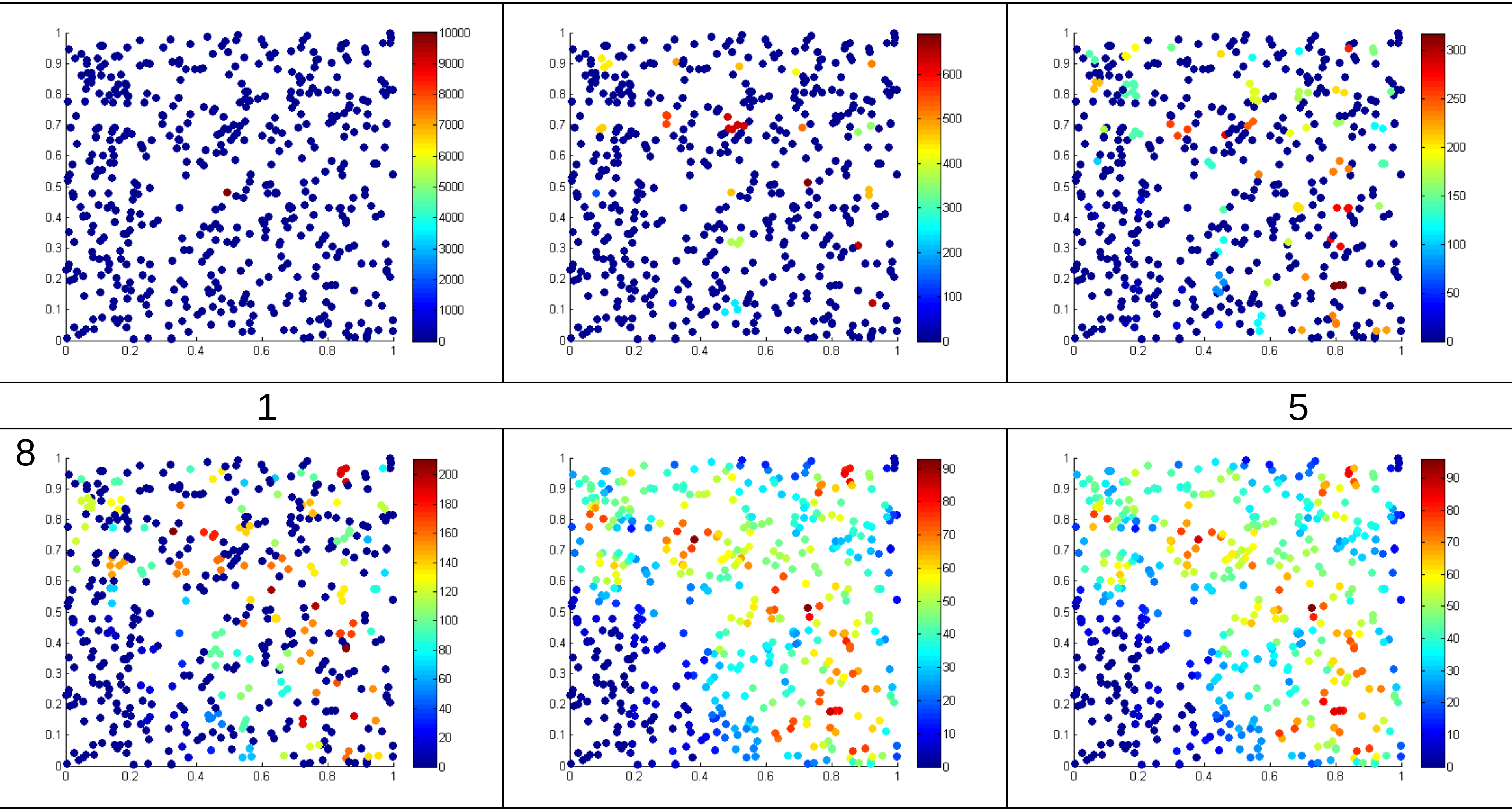
Neural Firing Across Resolutions



1

5

8

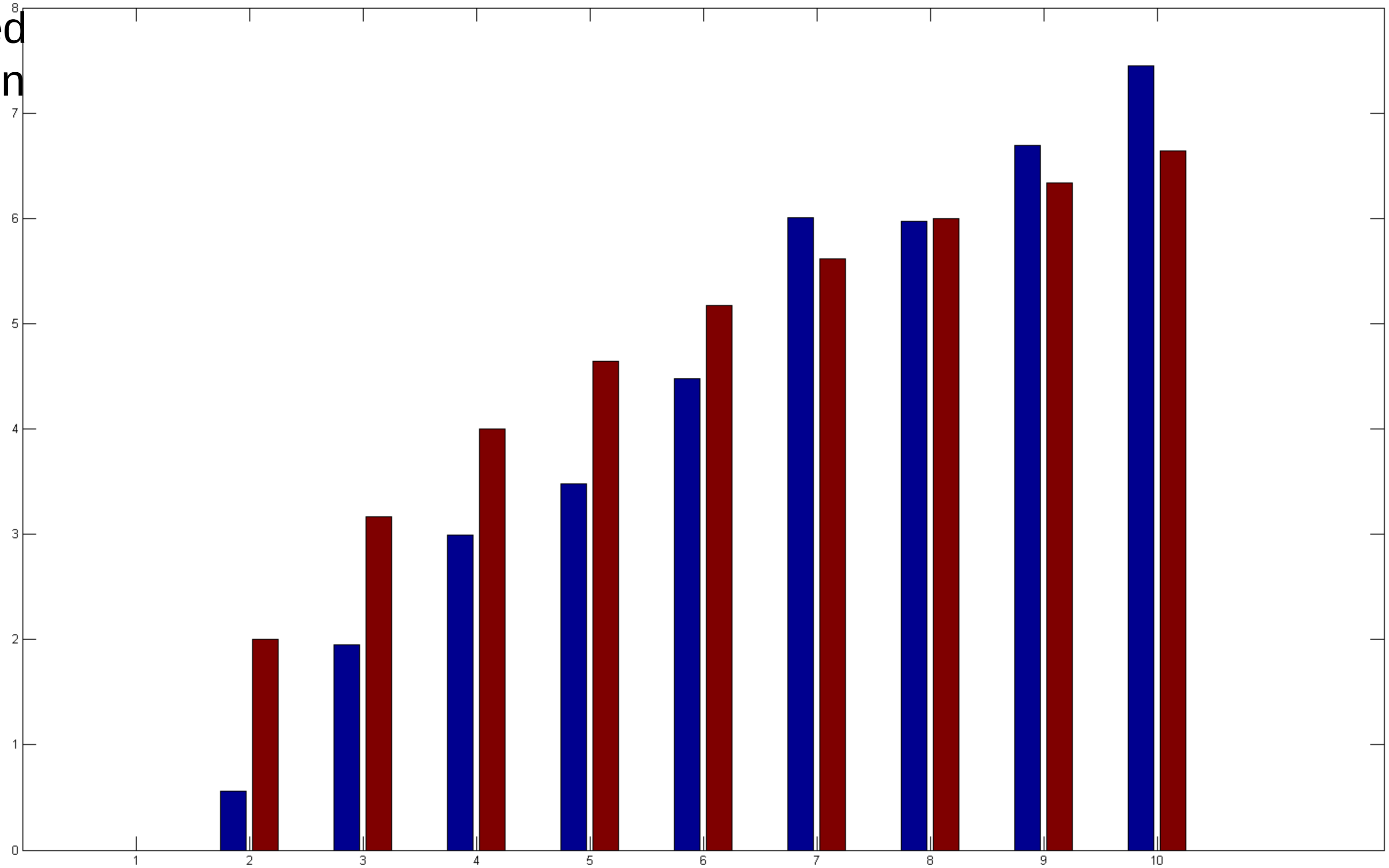
10

100

1000

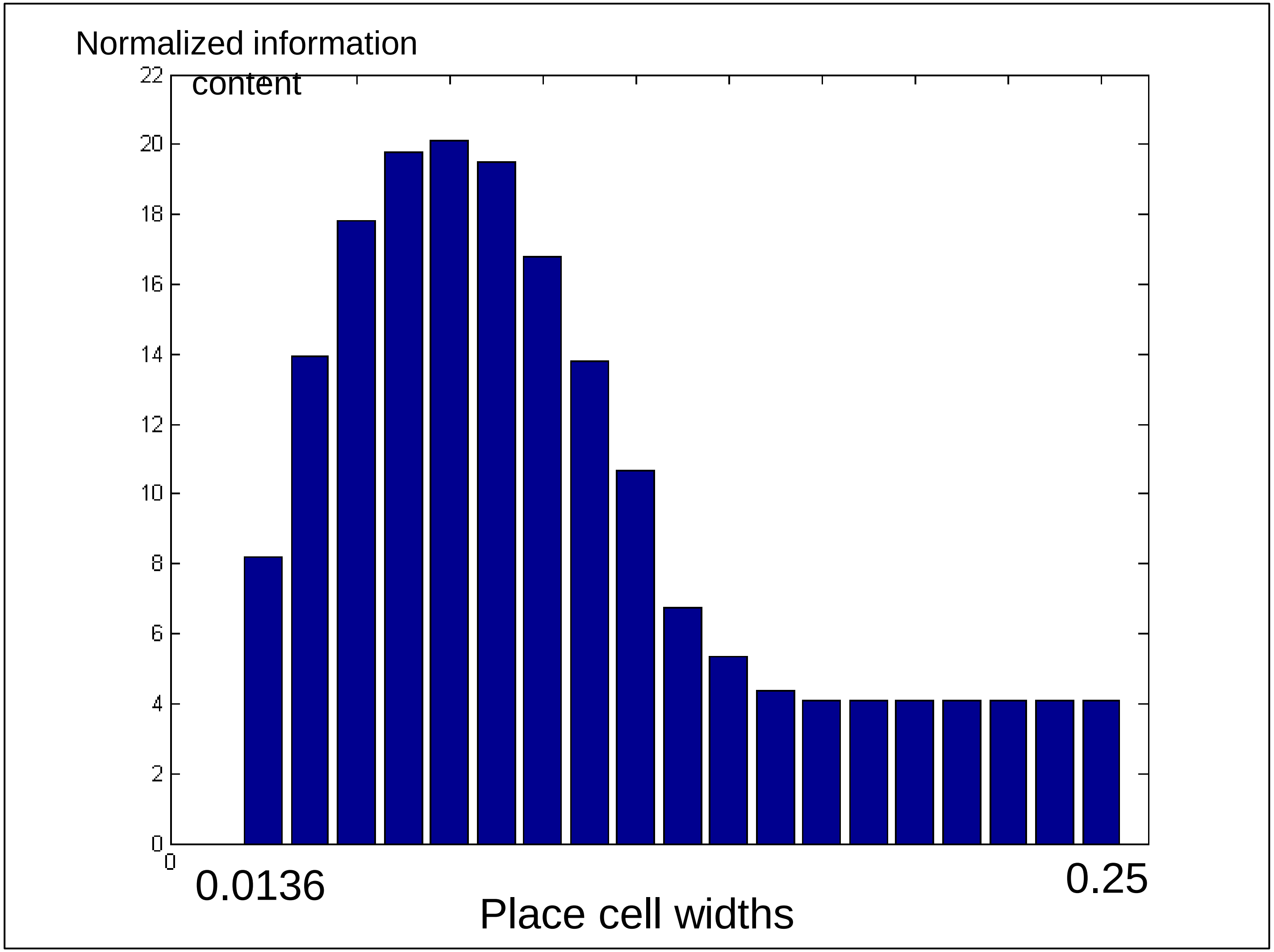
Resolutions 1-10

Normalized Information Content



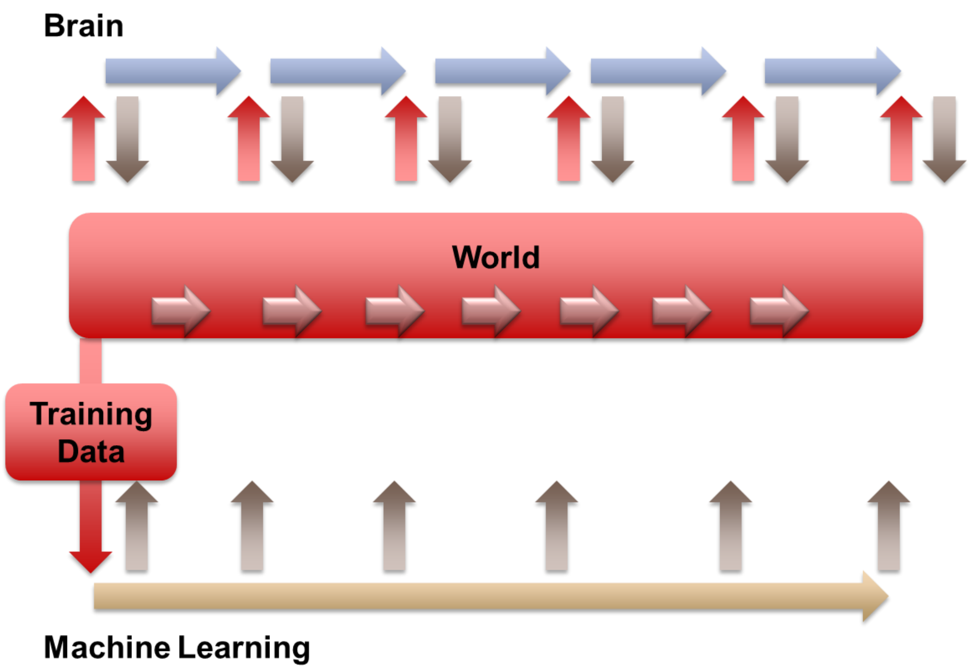
Sampling Resolution

Exploring Place Cell Widths



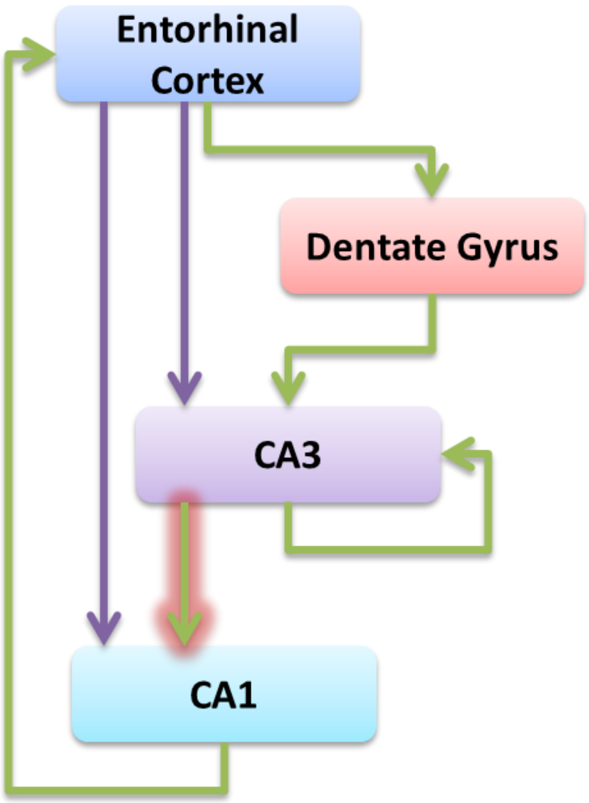
Motivation

- One of the differentiating capabilities of the brain is continuous learning
- So the question becomes where are we with respect to machine learning?
  - Most data-driven algorithms in ML do not continuously adapt



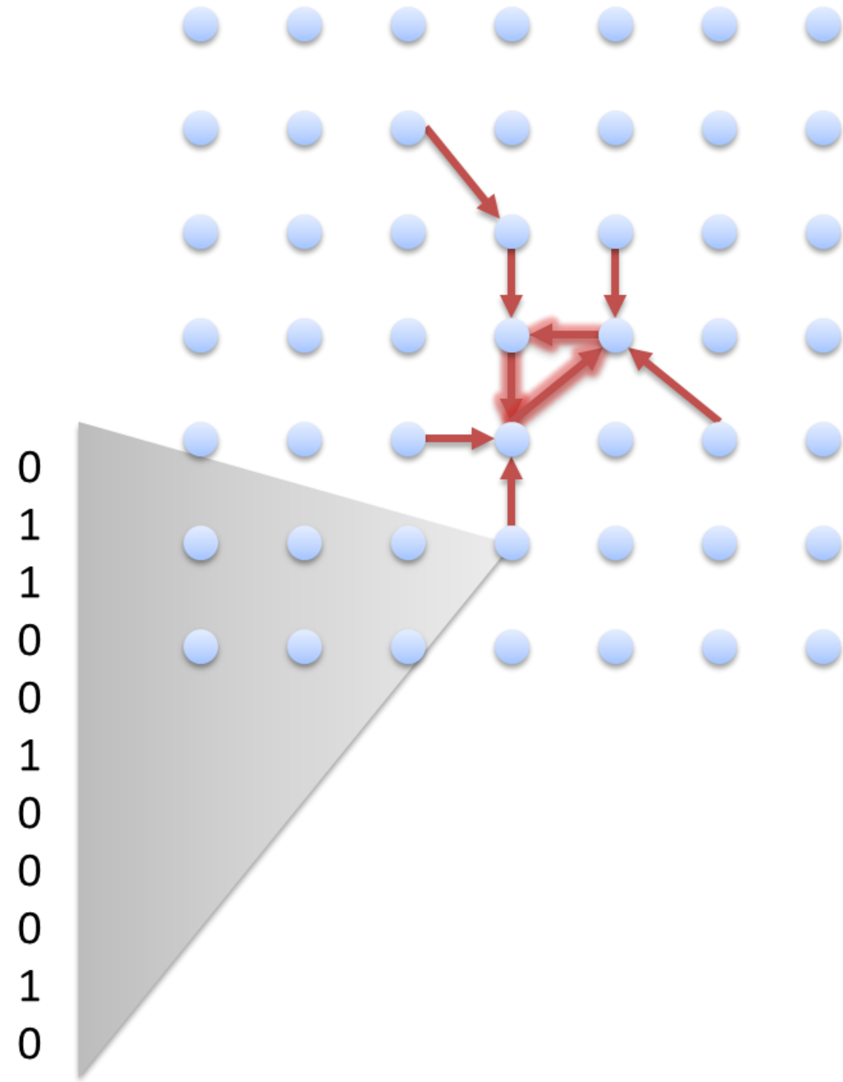
Modulation Model

- EC has high level cortical representations
- DG makes sparse, decorrelated mapping of EC
- CA3 is static dynamical “soup”
  - Limited recurrent plasticity
  - Recurrent dynamics provide a number of path attractors
  - EC->CA3 inputs are weak and modulatory
    - shift dynamical manifold
    - CA3 Attractors are positioned in context-dependent locations
  - DG inputs “seed” CA3 network which propagates to attractor basin
- CA1 “learns” to read CA3 attractors
  - Context dependent readout



Modulation Model

- Dynamics of ensembles of recurrently connected neurons form attractor “cycles”
  - Cycles can be sequences of states that acts as a ring attractor
  - A fixed point can be thought of as a cycle of size 1
- Temporal dynamical depth (e.g., spikes in flight) based representation would expand the number of possible states (2^{N*K}), but restrict the possible transitions between those states
- All stable points (either fixed points or points within a stable orbit) must be linearly independent
  - Effectively limited to less than N*K stable cycles, even though there are 2^{N*K} possible representations



Modulation Model

- One model of modulation is that attractor “structure” is the same but locations can move to different locations (see image)
- Modulation can be provided mechanistically by several sources
  - EC->CA3 inputs will bias some neurons more than others, thus shifting dynamical structure
  - Metabotrophic modulators (e.g., serotonin, acetylcholine) can bias neuronal timings and thresholds, which in turn shifts dynamics in a potentially reversable way