# State Space Models for Natural and Artificial Intelligence

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Leslie Valiant

# Why not study I?





# PROBABLY APPROXIMATELY CORRECT

Nature's Algorithms for Learning and Prospering in a Complex World

# **MARK** 53589083

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**Sensory inputs** 



Intelligent systems must maintain internal states to produce appropriate behavioral outputs



### Intelligent systems must maintain internal states to produce appropriate behavioral outputs

### **Sensory inputs**

In silico computation

Please write a Kalman filter in Python using JAX



### **Behavioral outputs**

### python import jax import jax.numpy as jnp # Kalman Filter Step Function def kalman\_filter\_step(state, params): # Unpack the state x, P = state # Unpack the parameters F, H, Q, R, z = params# Predict step x\_pred = jnp.dot(F, x) P\_pred = jnp.dot(F, jnp.dot(P, F.T)) + Q # Update step $y = z - jnp.dot(H, x_pred)$ S = jnp.dot(H, jnp.dot(P\_pred, H.T)) + R K = jnp.dot(P\_pred, jnp.dot(H.T \_\_\_\_)p.linalg.inv(S)))





# Exciting advances in neural and behavioral recording technologies

Large-scale neuronal measurements in freely behaving animals Automated tracking and computer vision for quantifying natural behavior



Jun, Steinmetz et al (2017).

Causal perturbations with closed-loop, patterned optogenetic stimulation









Pereira et al (2022)



# Exciting advances in machine learning models and computational hardware

# **Nobel Physics Prize Awarded for** Pioneering A.I. Research by 2 Scientists

With work on machine learning that uses artificial neural networks, John J. Hopfield and Geoffrey E. Hinton "showed a

# Nobel Prize in Chemistry Goes to 3 Scientists for Predicting and Creating Proteins

The Nobel, awarded to David Baker of the University of Washington and Demis Hassabis and John M. Jumper of Google



Transformer architecture

# Outline

- 1. Natural Intelligence: Internal states and attractor dynamics in the hypothalamus
- 2. Artificial Intelligence: Deep state space models for sequence-to-sequence modeling

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- 1. Natural Intelligence: Internal states and attractor dynamics in the hypothalamus
  - <u>Question</u>: How does the brain represent and maintain internal states?
  - <u>Method</u>: Recurrent switching linear dynamical systems (rSLDS)
  - <u>Results</u>: Intrinsic line attractor dynamics in the hypothalamus encode an aggressive internal state
  - <u>Extension</u>: Smoothly interpolating between states in an rSLDS
- 2. Artificial Intelligence: Deep state space models for sequence-to-sequence modeling

### Adi Nair





### Adi helped prepare some of the slides that follow.

## Collaborators

### David Anderson

### Ann Kennedy



# Optogenetic activation of neurons in the hypothalamus elicits attack behavior





Lee et al. (Nature, 2014)



# Miniscope imaging in VMHvI during spontaneous aggression shows mixed selectivity



Most neurons in VMHvI are tuned to intruder sex and are active during both sniffing and attack.

Remedios, Kennedy et al. (Nature, 2019) Karigo et al (Nature, 2021)



# Miniscope imaging in VMHvI during spontaneous aggression shows mixed selectivity

# Hypothesis An internal state of aggressiveness is encoded in the collective activity of neurons in the VMHvl.

Most

attack.

Remedios, Kennedy et al. (Nature, 2019) Karigo et al (Nature, 2021)



# Formalizing this hypothesis with a probabilistic model

### $oldsymbol{y}_t \in \mathbb{R}^N$ : neural population activity at time t



# Low-dimensional structure in neural data

If collective activity encodes a low-dimensional state (e.g., "aggressiveness"), the data should lie near a low-dimensional manifold.



### $oldsymbol{x}_t \in \mathbb{R}^D$ : continuous latent state (i.e., manifold coordinate)

## Low-dimensional structure in neural data

We think of neural activity as a noisy observation of a trajectory on the low-d manifold.



### $oldsymbol{x}_t \in \mathbb{R}^D$ : continuous latent state (i.e., manifold coordinate)

## Low-dimensional structure in neural data

We want to learn the dynamics that govern how trajectories unfold.





continuous state dim 1

# Computation through neural dynamics

Dynamical motifs are hypothesized to underlie various forms of neural computation.

rotational dynamics (e.g., motor control)



saddle point (e.g., winner-take-all)

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0		X	X	N	1	1	1	1	1	

continuous state dim 1

point attractor (e.g., memory) line attractor (e.g., integration)

continuous state dim 1

Adapted from Vyas et al. (2020)



# Computation through neural dynamics

Dynamical motifs are hypothesized to underlie various forms of neural computation.



# **Methodological Question**



continuous state dim 1

## How can we infer latent states and estimate their dynamics from **neural and behavioral** time series?



continuous state dim 1

Adapted from Vyas et al. (2020)





### Probabilistic state space models



### A spectrum of dynamics models

Limited capacity, Specialized inference, Data efficient, Easy to fit and understand.



### What can linear models do?



A lot! E.g., the motifs from before were all linear models, f(x) = Ax + b.

Moreover, linear systems are interpretable.

We can find analytical solutions for:

- fixed points
- stationary distribution (w/ Gaussian noise)
- dynamics along eigenmodes
- optimal control

### What **can't** linear models do?

Still, most computations require nonlinear dynamics.

bistability (e.g., decision making)



continuous state dim 1

continuous state dim 2





continuous state dim 1

### Key idea: nonlinear dynamics can often be approximated as piecewise-linear

Indeed, that's often how we analyze nonlinear dynamical systems!

bistability (e.g., decision making)



continuous state dim 1

continuous state dim 2

ring attractor (e.g., head direction)



continuous state dim 1

Limited capacity, Specialized inference, Data efficient, Easy to fit and understand.



### Switching linear dynamical systems (SLDS)



### Different linear dynamics in each discrete state



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> Ackerson and Fu (1970) Chang and Athans (1978) Ghahramani and Hinton (1996)

# Hamilton (1990) Murphy (1998) Fox et al (2009)

### Switching linear dynamical systems (SLDS)



Ackerson and Fu (1970) Chang and Athans (1978) Hamilton (1990) Ghahramani and Hinton (1996)

# Murphy (1998) Fox et al (2009)

### **Problem**: in an SLDS, discrete state transitions are independent of location!

### bistability (e.g., decision making)



continuous state dim 1

continuous state dim 2





continuous state dim 1

### **Recurrent** switching linear dynamical systems (rSLDS)



Linderman et al. (AISTATS, 2017) Zoltowski, Pillow, & Linderman (2020) ...and now many more



### Recurrent SLDS partition continuous state space into regions with linear dynamics



Linderman et al. (AISTATS, 2017) Zoltowski, Pillow, & Linderman (2020) ...and now many more



### A spectrum of dynamics models

Limited capacity, Specialized inference, Data efficient, Easy to fit and understand.



# rSLDS analysis reveals line attractor-like dynamics in VMHvl





# rSLDS analysis reveals line attractor-like dynamics in VMHvl









# rSLDS analysis reveals line attractor-like dynamics in VMHvl





Importantly, this is not true of all hypothalamic nuclei, e.g., MPOA.



# Dynamical systems explain individual differences in aggressiveness



### the stability of the attractor is enhanced in mice that are more aggressive

Nair et al. (Cell, 2023)



# Are these dynamics intrinsic to VMHvl or a read-out of an upstream region?



### No study has causally demonstrated the existence of intrinsic line attractor dynamics in mammals.



Amit Vinograd

Vinograd, Nair et al. (Nature, 2024)



# How can we gain access to the line attractor for perturbation?



2-photon holographic activation



line attractor neurons

"dream experiment"

Unfortunately, head-fixation results in loss of attack behavior.

Vinograd, Nair et al. (Nature, 2024)


# How can we gain access to the line attractor for perturbation?



VMHvI-Esr1 neurons are also active during observation of aggression (Yang et al., Cell 2023)

# How can we gain access to the line attractor for perturbation?



# VMHvI-Esr1 neurons are show line attractor dynamics during observation of aggression







Activation of  $x_1$  neurons should lead to integration if the line attractor is intrinsic.





\*Note: this requires fitting an rSLDS online, during the session, to design the perturbation.

Holographic on-manifold activation<sup>\*</sup> of line-attractor aligned  $x_1$  neurons leads to integration.





Holographic off-manifold activation of line-orthogonal x<sub>2</sub> neurons does not lead to integration.

Note: this requires fitting an rSLDS online, during the session, to design the perturbation.







on- and off-manifold perturbations provide first evidence of an intrinsic mammalian line attractor



## Do these attractor dynamics generalize to other internal state computations?



VMHvI shows attractor dynamics in female mice during mating, but only in proestrus.

Liu, Nair et al. (Nature, 2024)





Limited capacity, Specialized inference, Data efficient, Easy to fit and understand.



### Amber Hu

### David Zoltowski

### Lea Duncker







This collaboration has inspired new methodological work to address limitations of rSLDS

**Key idea:** parameterize f(x) as a Gaussian process with a novel kernel to produce smoothly switching linear dynamics.

Hu et al. (NeurIPS, 2024)



### Gaussian Process Stochastic Differential Equation (GP-SDE) Model

affine mapping to

high-d space



We propose a novel GP kernel to produce smoothly switching linear dynamics

Frigola et al. (NIPS, 2014) Duncker et al. (ICML, 2019) Course and Nair (Nature, 2023)



$$y(t) \sim PP(\exp(Cx(t) + d))$$





### A Gaussian Process prior for linear functions

Consider the following model for random linear functions  $f: \mathbb{R}^d \mapsto \mathbb{R}$ :

$$f(\mathbf{x}) = \mathbf{w}^{\top}(\mathbf{x} - \mathbf{c})$$
 intercept  
 $\mathbf{w} \sim N(\mathbf{0}, \mathbf{M})$  slope cova

Let 
$$\mathbf{f} = [f(\mathbf{x}_1), \dots, f(\mathbf{x}_n)]^ op$$
. Marginally, $\mathbf{f} \sim \mathrm{N}(\mathbf{0}, \mathbf{K})$ 

$$\mathbf{K} = \mathbf{\Phi} \mathbf{M} \mathbf{\Phi}^{ op} \qquad \mathbf{\Phi} = egin{bmatrix} \mathbf{x}_1 - \mathbf{c} \ dots \ \mathbf{x}_n - \mathbf{c} \end{bmatrix}$$

This is a **Gaussian process** with a **linear kernel!** 

$$K_{\text{lin}}(\mathbf{x},\mathbf{x}') = (\mathbf{x}-\mathbf{c})^{\top} \mathbf{M}(\mathbf{x}'-\mathbf{c})$$



### A Gaussian process model for linear dynamics functions

We can use GPs to define a prior on linear dynamics functions,  $f : \mathbb{R}^d \mapsto \mathbb{R}^d$ (Note: now it has a d-dimensional output.)

**Approach**: model each output dimension as an independent GP,

$$f_j \stackrel{\text{iid}}{\sim} \operatorname{GP}(0, K_{\text{lin}}(\cdot, \cdot)) \quad \text{for } j = 1, \dots, d$$

Assume the GPs share the same kernel hyperparameters. Then,

$$f(\mathbf{c}) = \mathbf{0} \quad (a.s.)$$

I.e., the intercept hyper-parameter defines the **fixed point** of the dynamics function.

Two samples of random linear dynamics functions:



### A Gaussian process model for **piecewise constant** functions

Let  $(\mathcal{A}_1, \ldots, \mathcal{A}_K)$  be a **partition** of  $\mathbb{R}^d$ .

Define a **one-hot** feature vector,

$$\pi(\mathbf{x}) = (\mathbb{I}[\mathbf{x} \in \mathcal{A}_1], \dots, \mathbb{I}[\mathbf{x} \in \mathcal{A}_K])^\top$$

The inner product defines of features defines a kernel,

$$K_{\pi}(\mathbf{x},\mathbf{x}') = \pi(\mathbf{x})^{\top}\pi(\mathbf{x}')$$

Samples  $f \sim \operatorname{GP}(0, K_{\pi}(\cdot, \cdot))$  yield **piecewise** constant functions.

Example draw from GP with p.c. kernel



### A Gaussian process that **smoothly interpolates** between piecewise constant functions

Let  $(\mathcal{A}_1, \ldots, \mathcal{A}_K)$  be a **partition** of  $\mathbb{R}^d$ .

Define a **one-hot** feature vector,

$$\pi(\mathbf{x}) = (\mathbb{I}[\mathbf{x} \in \mathcal{A}_1], \dots, \mathbb{I}[\mathbf{x} \in \mathcal{A}_K])^\top$$

The inner product defines of features defines a kernel,

$$K_{\pi}(\mathbf{x},\mathbf{x}') = \pi(\mathbf{x})^{\top}\pi(\mathbf{x}')$$

Samples  $f \sim \operatorname{GP}(0, K_{\pi}(\cdot, \cdot))$  yield **piecewise** constant functions.

More generally, suppose  $\pi(\mathbf{x}) \in \Delta_{K-1}$  varies smoothly. Then samples from the GP **smoothly interpolate** between **piecewise constant** functions. Example draw from GP with p.c. kernel



$$\pi_1(\mathbf{x}) = \sigma((x_1^2 + x_2^2 - 1)/\tau)$$

### A Gaussian process kernel for smoothly switching linear dynamics





Revisiting the VMHvI neural population activity from Nair et al. (2023) with a GP-SLDS, now we can quantify uncertainty in the latent state dynamics estimates.

GP-SLDS provides uncertainty estimates for the dynamics and posterior probability of attractors.

Hu et al. (NeurIPS, 2024)



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- 2. Artificial Intelligence: Deep state space models for sequence-to-sequence modeling

# Outline

- 1. Natural Intelligence: Internal states and attractor dynamics in the hypothalamus
- 2. Artificial Intelligence: Deep state space models for sequence-to-sequence modeling
  - <u>Question</u>: Can simple compositions of linear systems perform more complex computations?
  - <u>Method</u>: Simple state space layers with parallel scans (S5)
  - <u>Results</u>: Impressive performance on long-range sequence modeling tasks
  - <u>Extension</u>: Towards scalable and stable parallelization of nonlinear RNNs

# Acknowledgements

### Jimmy Smith





### Andy Warrington

### Xavier Gonzalez



Inspired by work of Albert Gu, Tri Dao, Chris Ré, and others.





### Recurrent neural networks

(Note: Everything is deterministic in this picture.)



RNNs allow fast autoregressive generation, but evaluation ("inference") is inherently sequential.





Transformers allow fast parallel evaluation — this may be the biggest reason for their success. However, autoregressive generation is costly.

### Transformers

### What if we restrict ourselves to **linear** recurrent neural networks?



 $x_t = \mathbf{A}x_{t-1} + \mathbf{B}u_t$  $y_t = \mathbf{C}x_t$ 



### Linear RNNs are equivalent to convolutions



$$y_t = \mathbf{C}\mathbf{A}^t\mathbf{B}u_0 + \mathbf{C}\mathbf{A}^{t-}$$

$$\mathbf{y} = \mathbf{K} \circledast \mathbf{u}$$
  
 $\mathbf{K} = (\mathbf{CB}, \mathbf{C})$ 

 $^{-1}\mathbf{B}u_1 + \ldots \mathbf{CAB}u_{t-1} + \mathbf{CB}u_t$  $\left| \right|$ 

 $CAB, \ldots CA^{T-1}B)$ 

Linear RNNs allow fast autoregressive generation and fast parallel evaluation (via convolution)!



Linear state space layers are linear in time but nonlinear in depth.

Gu et al (2021) proposed S4, which stacks linear state space layers with nonlinearities in between







### But the devil is in the details...

### With **\$5**, we aimed to simplify \$4 by sticking in the time domain and using **parallel scans.**





How can we parallelize the sequential evaluation?



### With **S5**, we aimed to simplify S4 by sticking in the time domain and using **parallel scans**.

 $\Rightarrow$ 

![](_page_61_Figure_1.jpeg)

### A pair of linear updates is still linear!

We use complex diagonal matrices to avoid cubic cost.

![](_page_61_Figure_4.jpeg)

![](_page_61_Picture_6.jpeg)

### With **S5**, we aimed to simplify S4 by sticking in the time domain and using **parallel scans**.

![](_page_62_Figure_1.jpeg)

Applying this update in parallel and recursively allows us to compute the entire state sequence in O(log T) time on a parallel machine.

![](_page_62_Picture_5.jpeg)

### S5 performs very well on machine learning benchmarks, including Path-X

Model	ListOps	Text	Retrieval	Image	Pathfinder	Path-X	Avg.
(Input length)	$(2,\!048)$	(4,096)	(4,000)	(1,024)	(1,024)	(16, 384)	
Transformer	36.37	64.27	57.46	42.44	71.40	X	53.6
Luna-256	37.25	64.57	79.29	47.38	77.72	X	59.3
H-Trans1D	49.53	78.69	63.99	46.05	68.78	X	61.4
CCNN	43.60	84.08	X	88.90	91.51	X	68.0
Mega $(\mathcal{O}(L^2))$	63.14	90.43	91.25	90.44	96.01	<u>97.98</u>	88.2
Mega-chunk $(\mathcal{O}(L))$	58.76	90.19	90.97	85.80	94.41	93.81	85.6
S4D-LegS	60.47	86.18	89.46	88.19	93.06	91.95	84.8
S4-LegS	59.60	86.82	90.90	88.65	94.20	96.35	86.0
Liquid-S4	62.75	89.02	91.20	89.50	94.8	96.66	87.3
<b>S</b> 5	62.15	89.31	91.40	88.00	95.33	98.58	87.4

![](_page_63_Picture_3.jpeg)

### S5 tops leaderboards for neural prediction benchmarks too!

![](_page_64_Figure_1.jpeg)

*Table 1:* Co-smoothing (in units of bits-per-spike) metric on MC Maze and DMFC RSG benchmarks [Pei *et al.*, 2021] for S5 compared to SOTA methods. Note: we exclude ensemble methods and only consider single models.

ıod	MC Maze()	DMFC RSG (↑)		
Ours)	0.3826	0.1981		
ADS	0.3748	N/A		
ЪТ	0.3691	0.1859		
-VAE	0.3559	N/A		
al RoBERTa	0.3551	N/A		
f	0.3382	0.1781		
LFADS	0.3364	0.1829		
Г	0.3304	0.1821		
	0.3229	0.1720		
3	0.2249	0.1243		

### Unlike convolutions, the S5 parallel scan also allows for different dynamics at each time point

Gu and Dao (2023) exploited this property in Mamba, which uses input-dependent dynamics.

![](_page_65_Picture_2.jpeg)

### Back to RNNs... are they really so sequential?

![](_page_66_Figure_1.jpeg)

**Idea**: What if we linearize f around a current guess of the latent states?

$$f(x_t) \approx f(x_t^{(i)}) + \frac{\partial f}{\partial x}(x_t^{(i)})(x_t - x_t^{(i)}) \triangleq \hat{f}(x_t; x_t^{(i)})$$

Then we can use parallel scan to solve for the states, linearize again, and repeat. This is the Gauss-Newton method. Lim et al (2024) called it **DEER**.

![](_page_66_Figure_5.jpeg)

Gonzalez et al. (NeurIPS, 2024)

![](_page_66_Picture_7.jpeg)

![](_page_67_Figure_0.jpeg)

Gauss-Newton can be unstable! Levenberg-Marquardt introduces a trust region, which turns this into a Kalman filtering problem.

We call this method ELK.

Gonzalez et al. (NeurIPS, 2024)

![](_page_67_Picture_5.jpeg)

![](_page_68_Figure_1.jpeg)

Quasi-DEER is faster and more memory efficient with diagonal Jacobian approximations

Gonzalez et al. (NeurIPS, 2024)

![](_page_68_Picture_4.jpeg)

### (Quasi-DEER) becomes numerically unstable when the linear approximation diverges

![](_page_69_Figure_1.jpeg)

Parallel Iteration 0

### ELK addresses this limitation by introducing a trust region

![](_page_70_Figure_2.jpeg)

### Parallel Iteration 0

# Conclusions

- are for you!
- ML and beating benchmarks for long-range sequence modeling.

• Whether you're interested in biological or artificial intelligence, state space models

• With modern methods for measuring and perturbing brain activity, we can fit SSMs at scale, test their predictions, and start to elucidate underlying circuit methods.

• Perhaps surprisingly, the humble linear dynamical system is making a comeback in

• There is lots of exciting (and very interdisciplinary) work to be done on both fronts.
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		6

https://github.com/lindermanlab

https://web.stanford.edu/~swl1/

### <u>Collaborators</u>

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## Not all hypothalamic nucleii exhibit line attractor-like dynamics



rSLDS analysis of MPOA finds faster time-locked motor behavior related dimensions

Nair et al. (Cell, 2023)



# How can we gain access to the line attractor for perturbation?



# VMHvI-Esr1 neurons are show line attractor dynamics during observation of aggression

Vinograd, Nair et al. (Nature, 2024)



# What mechanisms give rise to the line attractor?

## Line attractors are notoriously fragile and require precise fine-tuning.



# spiking neural networks with slow neurotransmitter release can create robust line attractors with time constants seen in data

Vinograd, Nair et al. (Nature, 2024)



## What mechanisms give rise to the line attractor?



selective functional connectivity among line attractor-aligned x<sub>1</sub> neurons

Vinograd, Nair et al. (Nature, 2024)



## What mechanisms give rise to the line attractor?

### "CRISPRscope" for cell-type specific perturbation of neuropeptide receptors + neural imaging



Removal of OXT/AVP receptors eliminates integration & line attractor dynamics in VMHvI.



Mountoufaris et al. (Cell, 2024)



## Unlike convolutions, S5 also allows for different dynamics at each time point



Model	Relative speed	Regression MSE $(\times 10^{-3})$
mTAND*	8.3 imes	$65.64 \pm 4.05$
RKN*	1.3  imes	$8.43\pm0.61$
RKN- $\Delta_t^*$	1.3  imes	$5.09\pm0.40$
ODE-RNN*	0.68  imes	$7.26 \pm 0.41$
CRU*	0.68  imes	$4.63\pm1.07$
CRU (our run)	$1.00 \times$	$\underline{3.81} \pm \underline{0.28}$
S5	130  imes	$\textbf{3.38} \pm \textbf{0.28}$

With different A's for each time step, we can handle irregularly sampled, continuous time data.

Smith et al. (ICLR, 2023)

