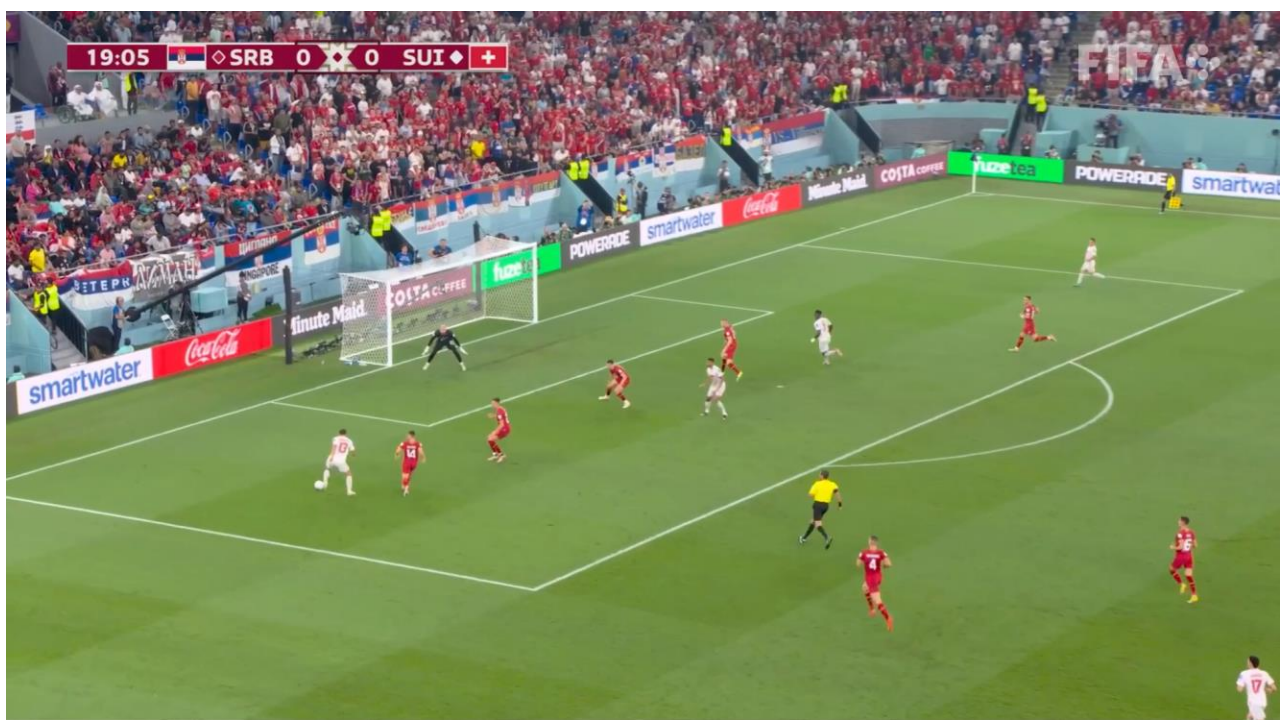


# **NX-435**

# **NeuroAI**

Prof. Mackenzie Mathis, PhD  
Spring 2025

# Biological Intelligence ↔ Artificial Intelligence



World Cup 2022 CH



DeepMind 2023

This is still a large gap in our ability to build adaptive embodied AI

***Of course, artificial Intelligence has made huge leaps with LLMs...***



tell me a joke about Swiss soccer players vs. DeepMind robots playing soccer




# Dogs or Muffins?




Slide courtesy of Prof. Andreas Tolias

Karen Zack (art director)








please tell me what is in each cell in a tabular format aligned with this picture grid.


Here's the content of each cell in the provided image, organized in a tabular format:

	1	2	3	4	5	6
1	Muffin	Dog	Muffin	Muffin	Dog	Muffin
2	Dog	Dog	Muffin	Dog	Dog	Muffin
3	Muffin	Dog	Muffin	Muffin	Dog	Muffin
4	Dog	Dog	Dog	Muffin	Dog	Dog
5	Muffin	Dog	Muffin	Dog	Dog	Muffin
6	Dog	Dog	Muffin	Dog	Dog	Muffin

This table identifies each cell as either a muffin or a dog, corresponding to the grid in the image.

A please tell me what is in each cell in a tabular format aligned with this picture grid.






◆ Certainly! Here's a tabular representation of the image content, aligned with the grid:

Show drafts

Row	Column 1	Column 2	Column 3	Column 4	Column 5
1	Muffin	Chihuahua	Muffin	Chihuahua	Muffin
2	Chihuahua	Muffin	Chihuahua	Muffin	Chihuahua
3	Chihuahua	Muffin	Chihuahua	Muffin	Chihuahua
4	Chihuahua	Muffin	Chihuahua	Muffin	Chihuahua





A please tell me what is in each cell in a tabular format aligned with this picture grid.

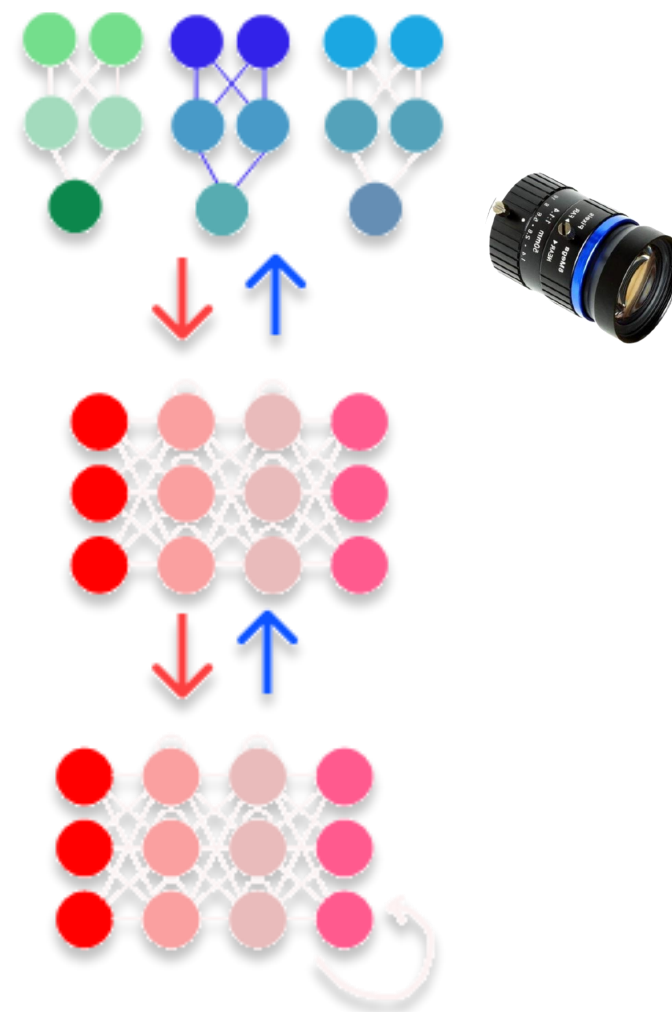
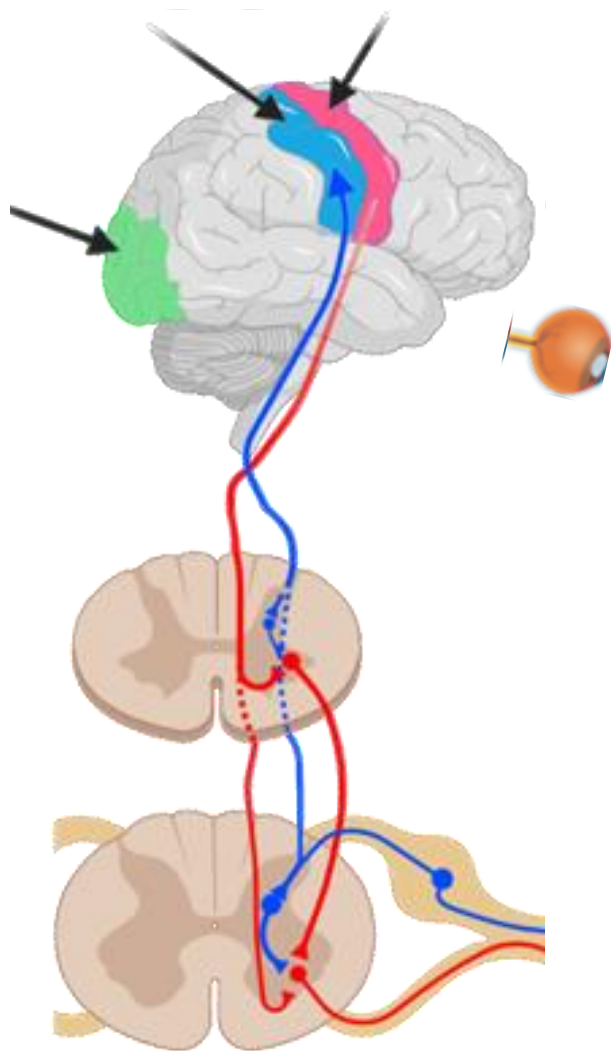
I'll describe the contents of each cell in a tabular format that aligns with the 4x8 grid shown in the image:

Muffin	Dog	Dog	Dog	Muffin	Dog	Dog	Dog
Dog	Muffin	Dog	Muffin	Dog	Dog	Muffin	Dog
Dog	Dog	Dog	Dog	Dog	Dog	Dog	Dog
Dog	Muffin	Dog	Muffin	Dog	Muffin	Dog	Muffin

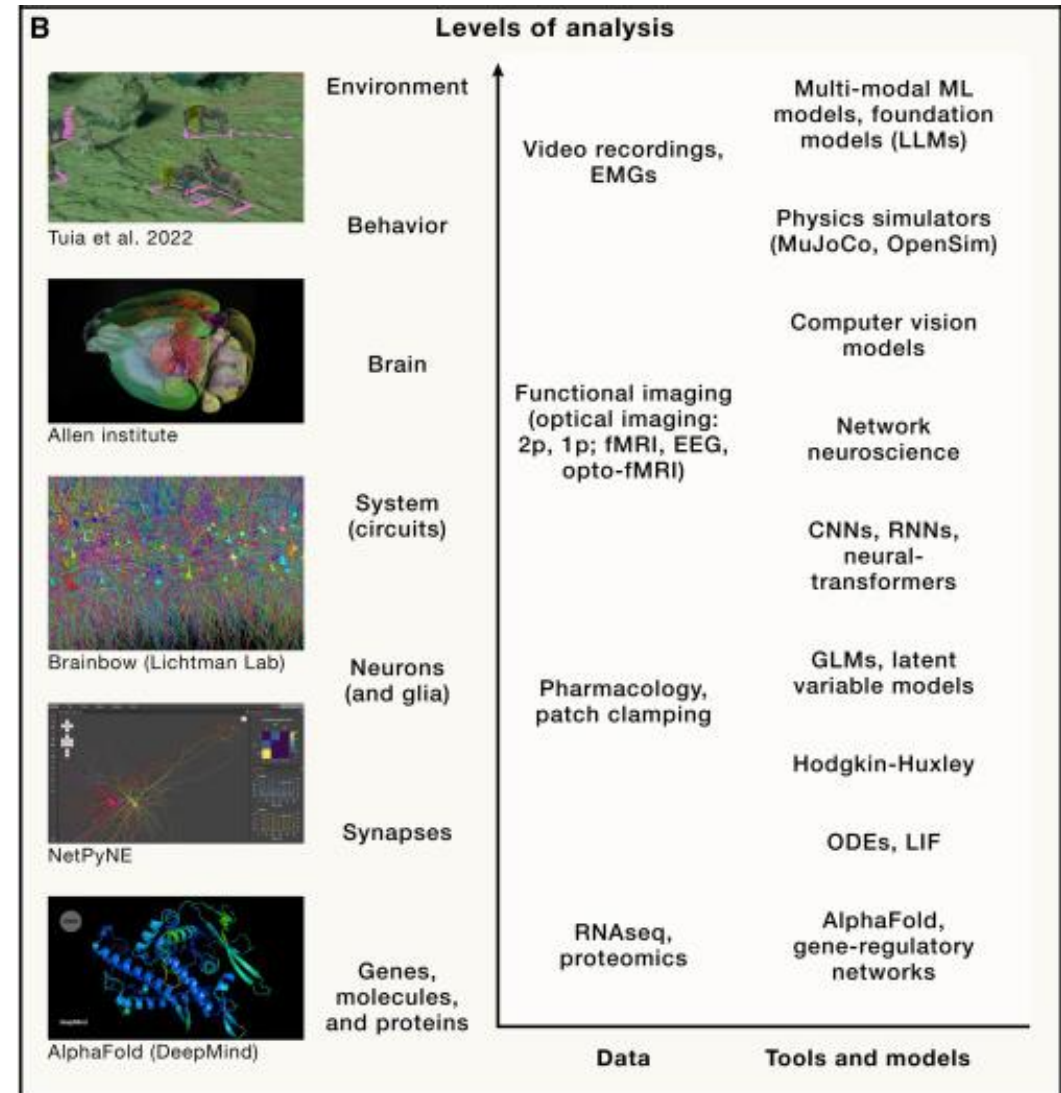
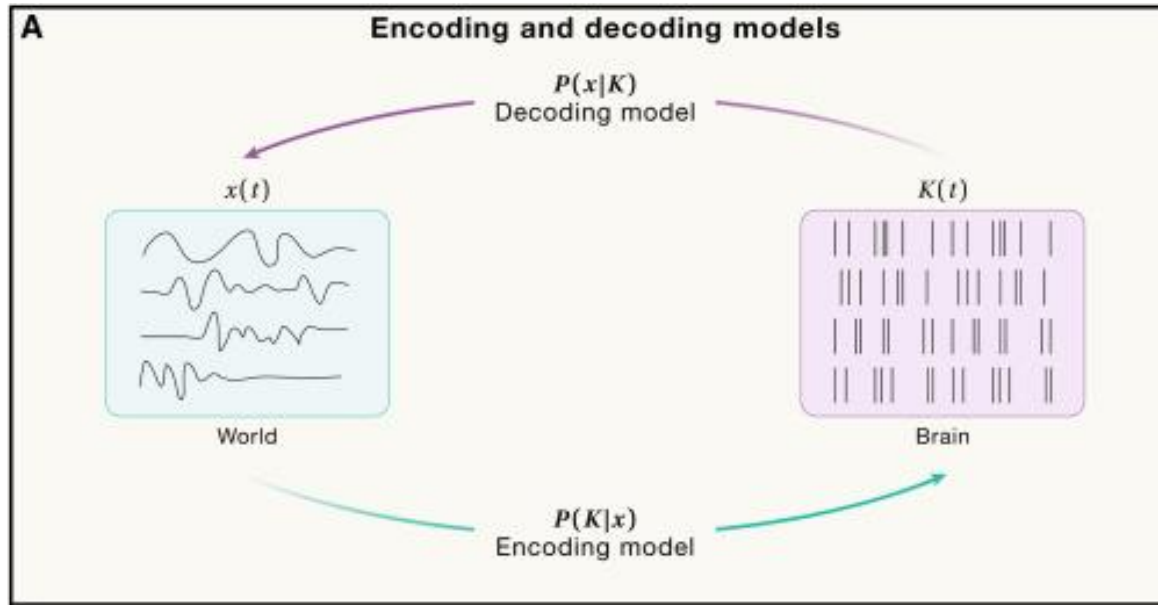


Slide courtesy of Prof. Andreas Tolias

# Biological Intelligence ↔ Artificial Intelligence



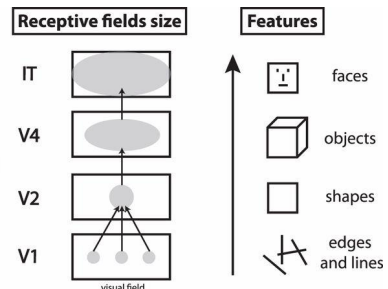
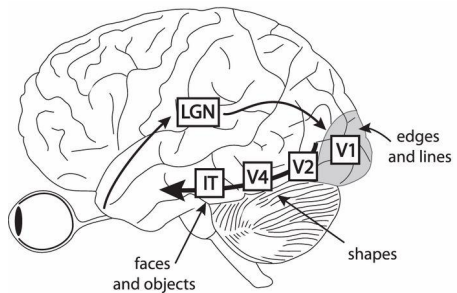
# Biological Intelligence ↔ Artificial Intelligence





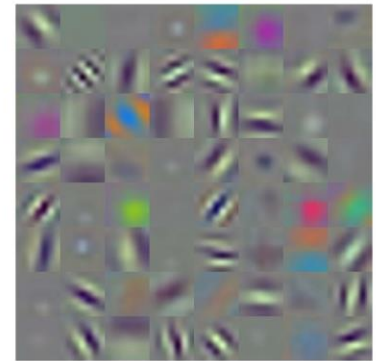
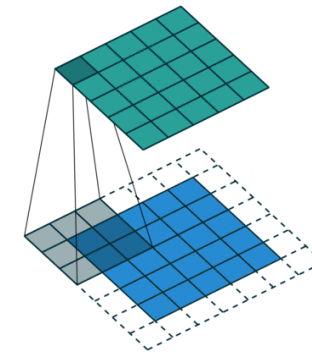
# What is neuroAI?

Neuroscience



Hubel & Wiesel discoveries in cat  
V1 inspired convolutional neural  
networks

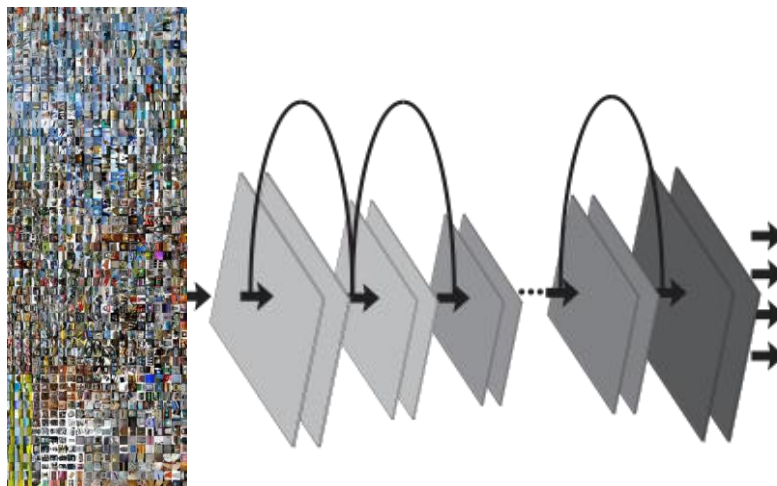
Artificial Intelligence (AI)



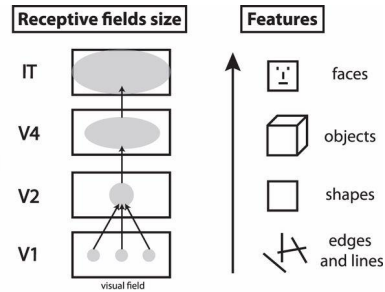
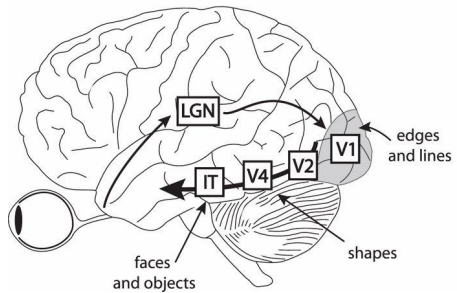
Convolutions  
(CNN)

Representations  
in ImageNet  
trained (CNN)

cat

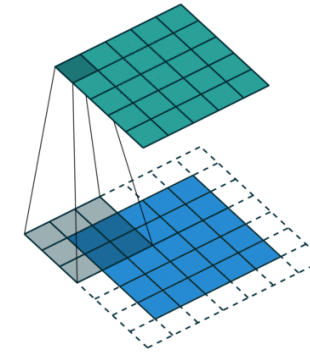


# Neuroscience

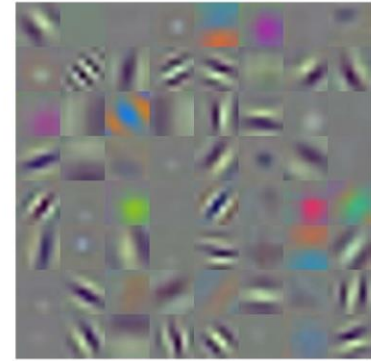


Hubel & Wiesel discoveries in cat  
V1 inspired convolutional neural  
networks

# Artificial Intelligence (AI)



Convolutions  
(CNN)

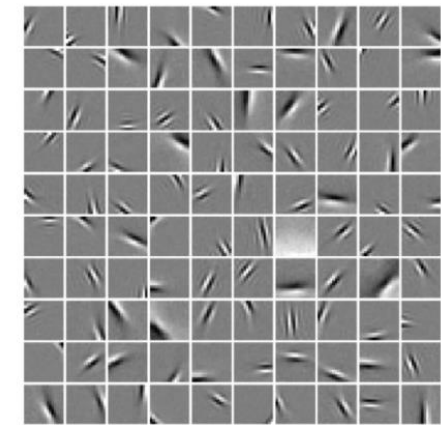
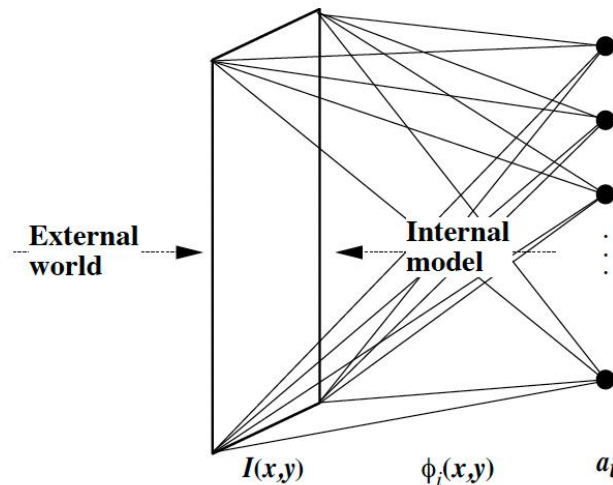


Representations  
in ImageNet  
trained (CNN)

edge detector neurons  
can be explained with  
sparse autoencoding

$$I(x, y) = \sum_i a_i \phi_i(x, y) + \epsilon(x, y)$$

*Adapted from A. Mathis*

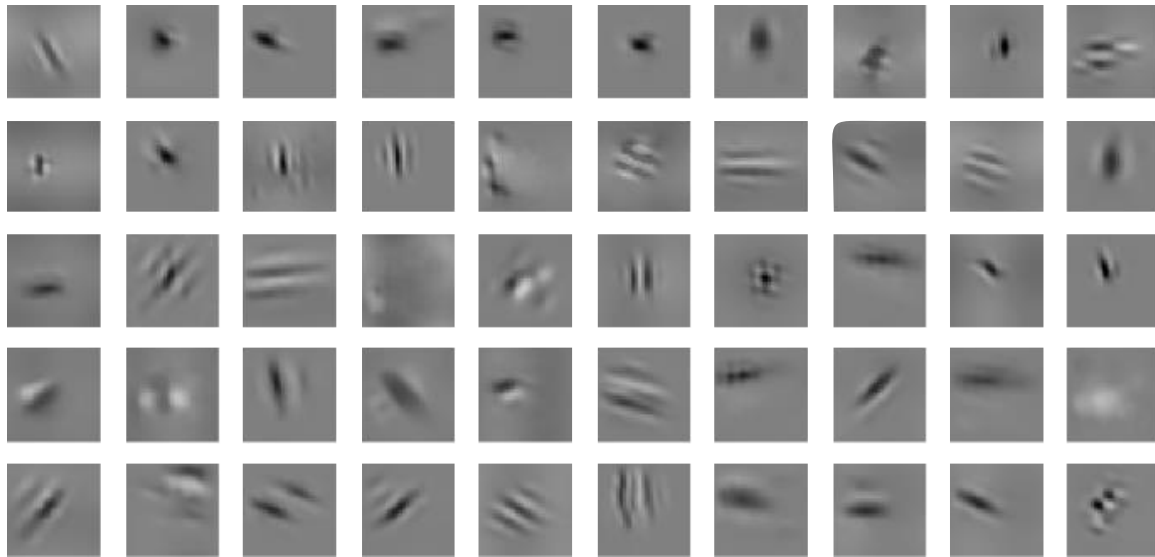


$\phi_i(x, y)$

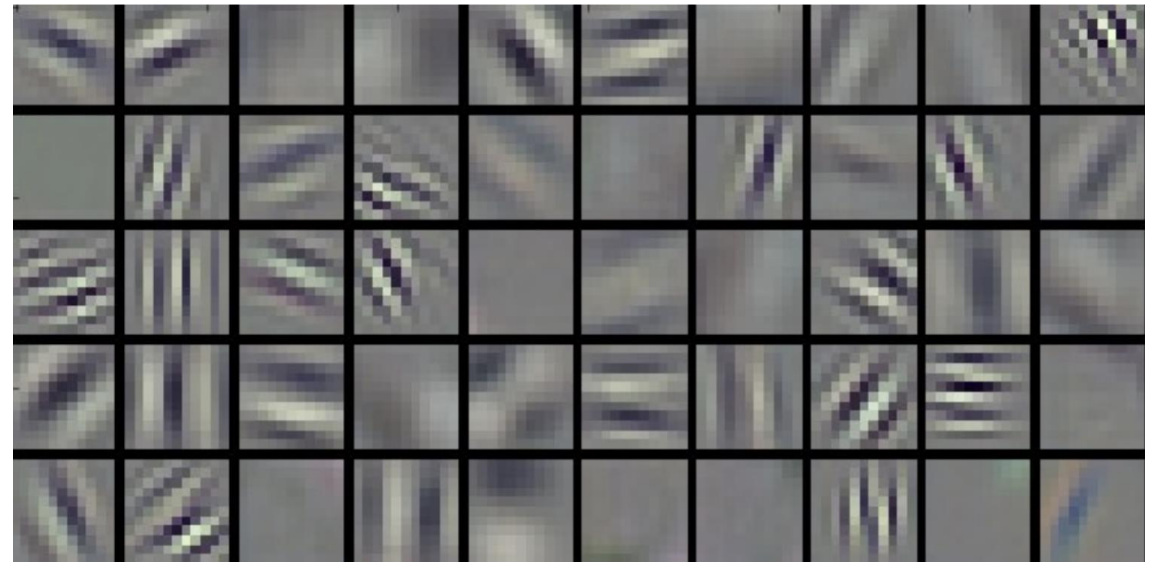
Olshausen & Field, 1996 Nature

# Universality of Representations

feature detectors in macaque V1



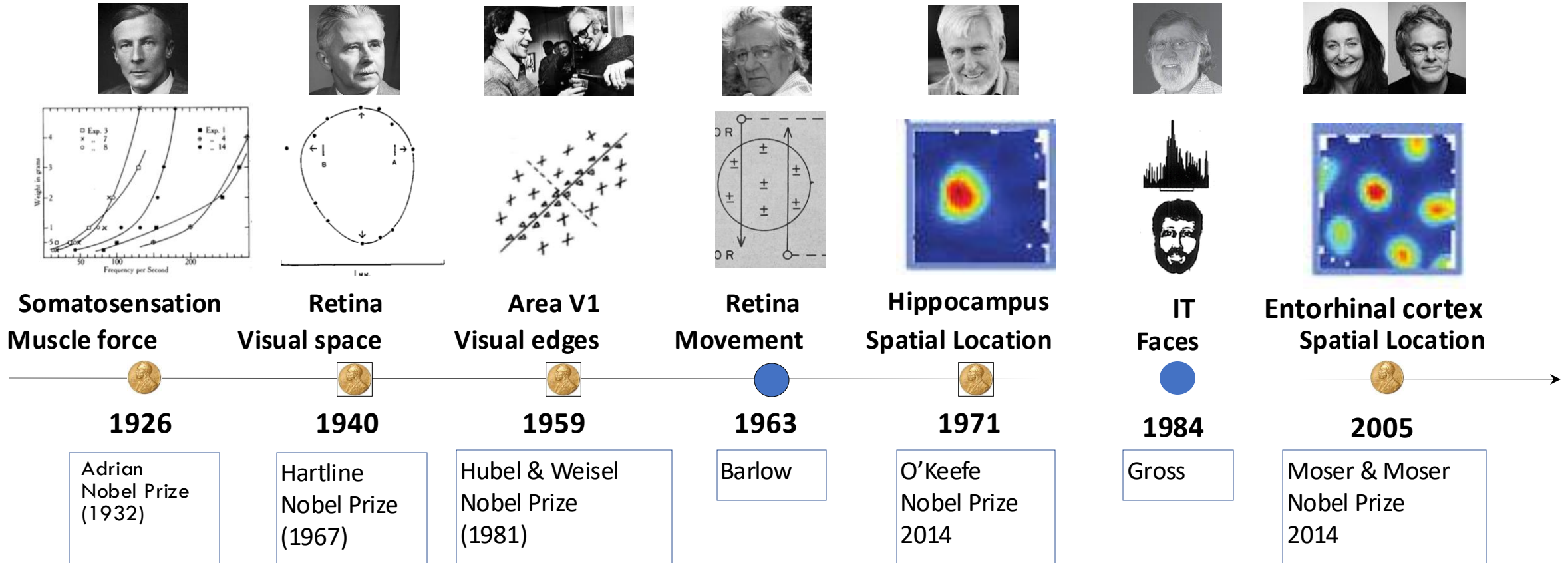
feature detectors in CNNs





# The representational level

Equivalences between neural activity and sensory input & behavior



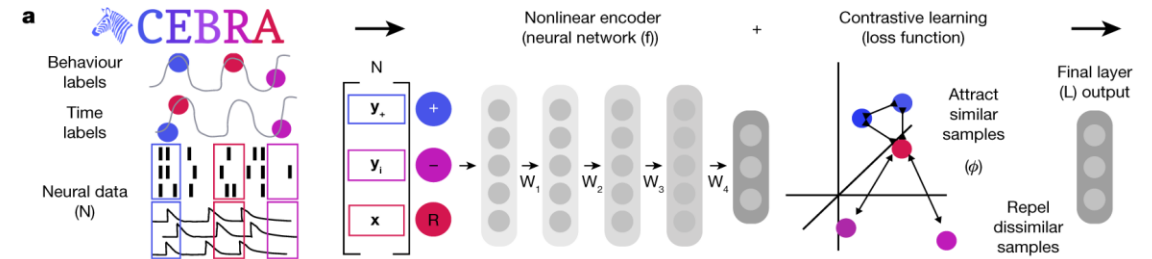
# What is neuroAI?

Neuroscience

Artificial Intelligence (AI)



Data: Chowdhury  
et al 2020 eLife



Schneider, Lee,  
Mathis 2023 Nature

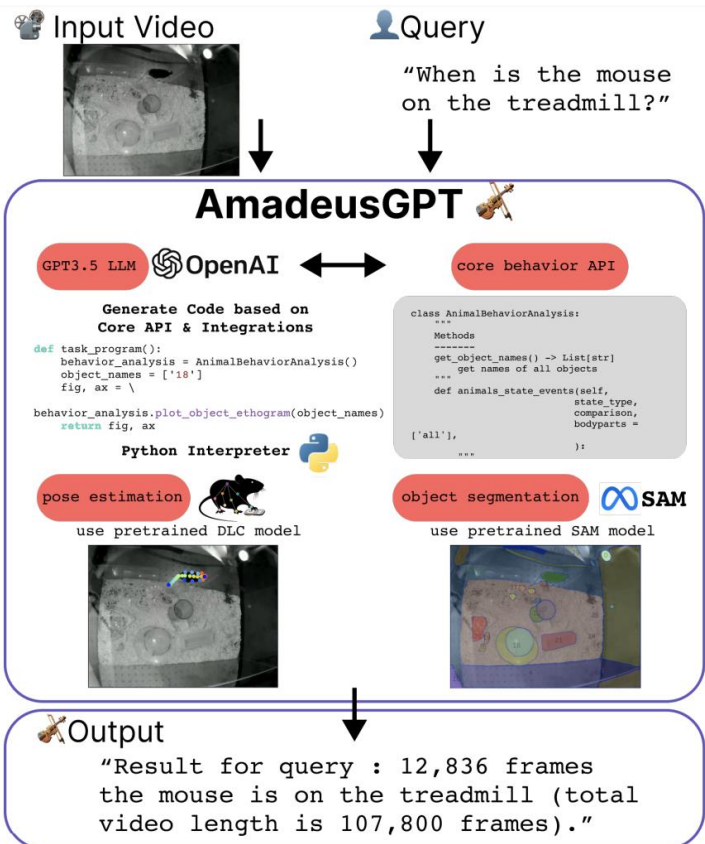
Which lead to better neural  
dynamical models of sensorimotor  
cortex (important for fundamental  
understanding and BCIs)

Advances in AI, such as  
**contrastive learning** in image  
processing could be expanded  
to neuro-specific domains



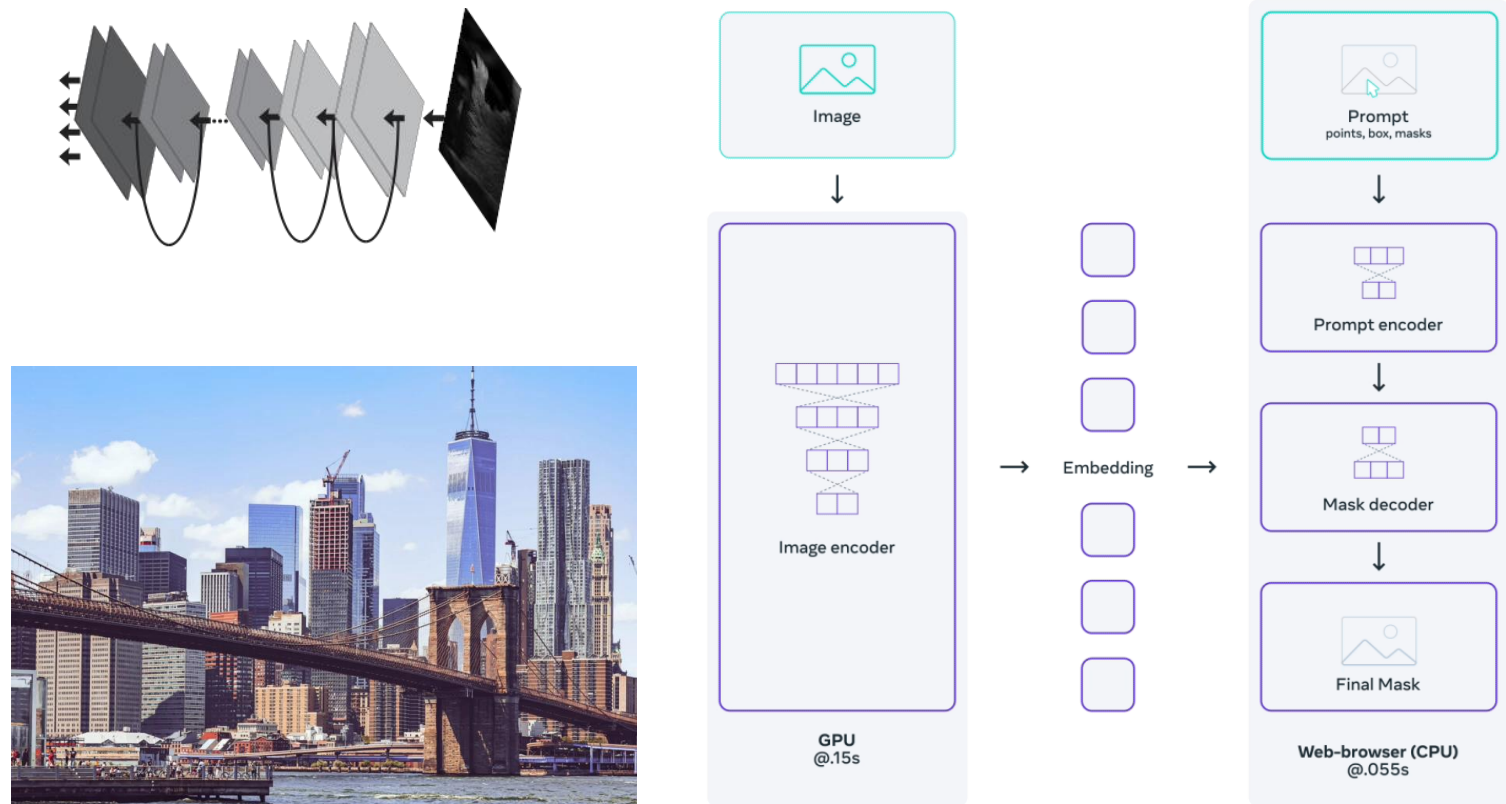
# What is neuroAI?

Neuroscience



AmadeusGPT Ye et al. 2023

Artificial Intelligence (AI)

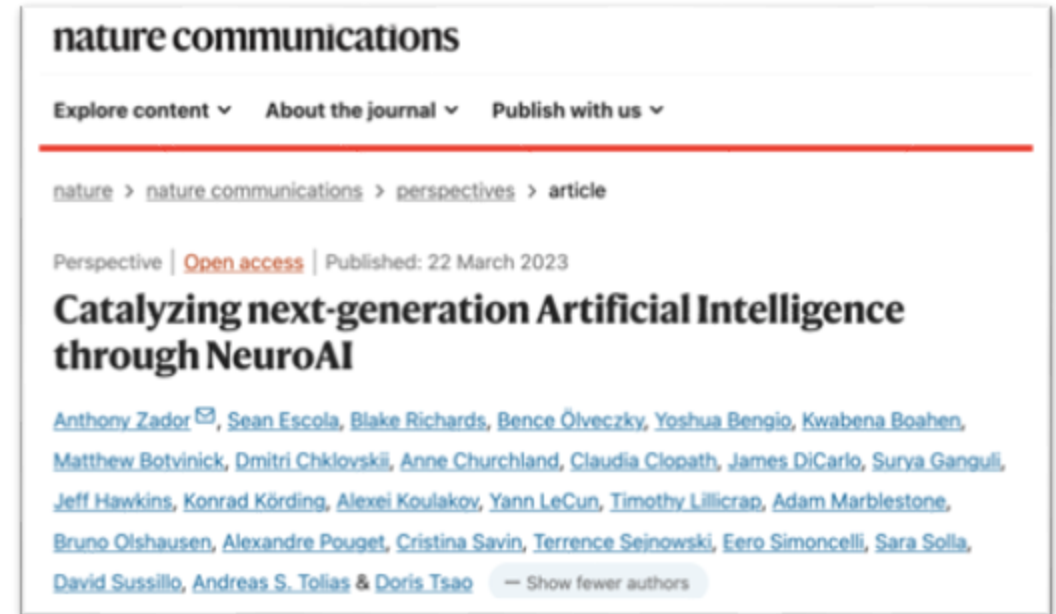


Segment Anything (Meta AI)

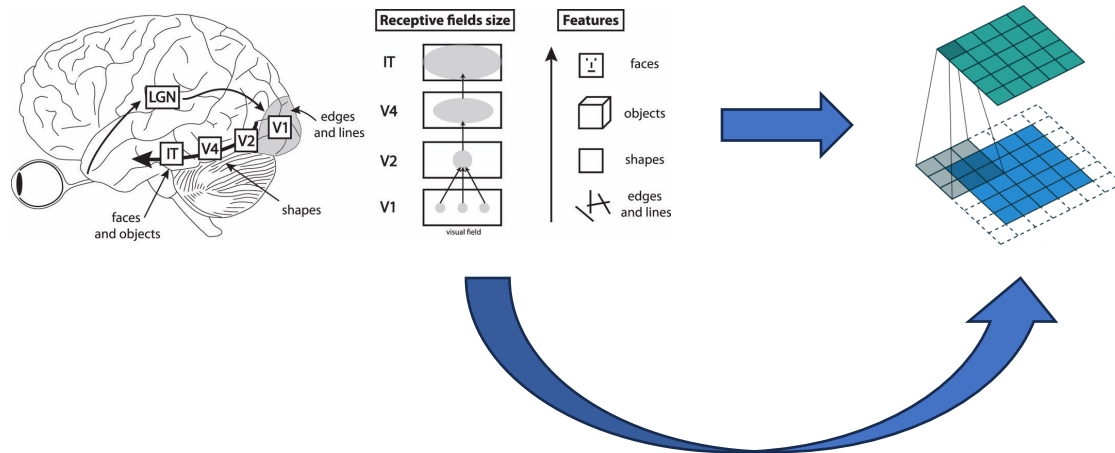


# What is neuroAI:

- Many definitions, but widely accepted that it is the **new inter-disciplinary field of merging neuroscience and AI research** ( $\leftrightarrow$ )
- Others define it more narrowly as using neuroscience ( $\rightarrow$ ) to shape research in AI

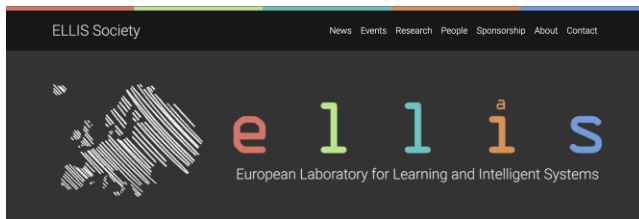


# One rapidly growing area is trying to build **better AI** by better **understanding Biological Intelligence (BI) / Natural Intelligence (NI)**



How can we build better models of neural systems, and what is the role of systems neuroscience?

<https://ellis.eu/programs/natural-intelligence>



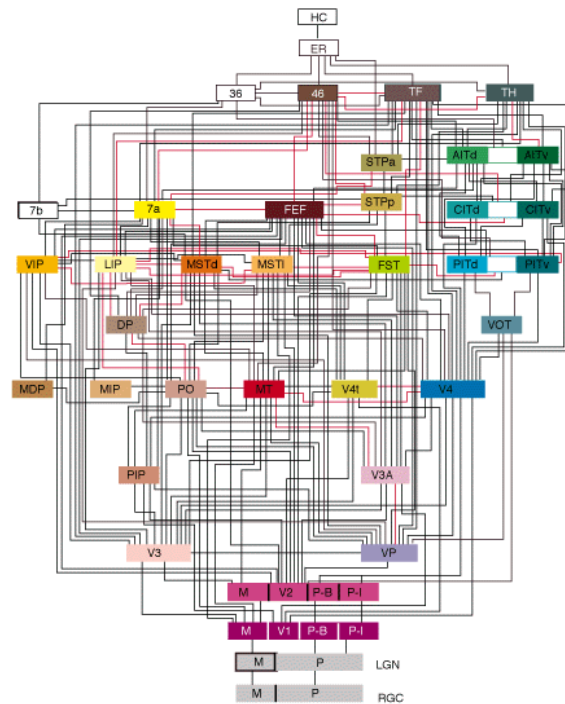
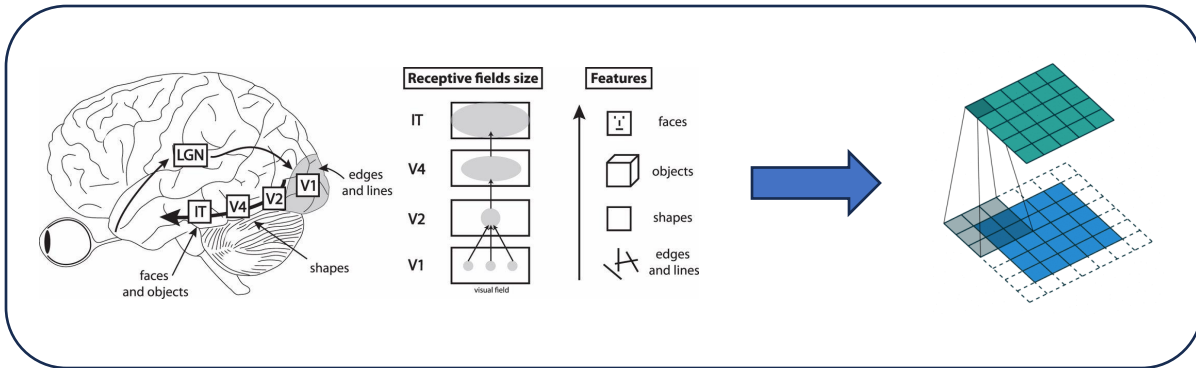
*\*note, ELLIS also has the top umbrella PhD program in Europe for ML/AI research*

- “If a new facet of biological computation found to be critical to supporting a cognitive function, then we would consider it an excellent candidate for incorporation into artificial systems”

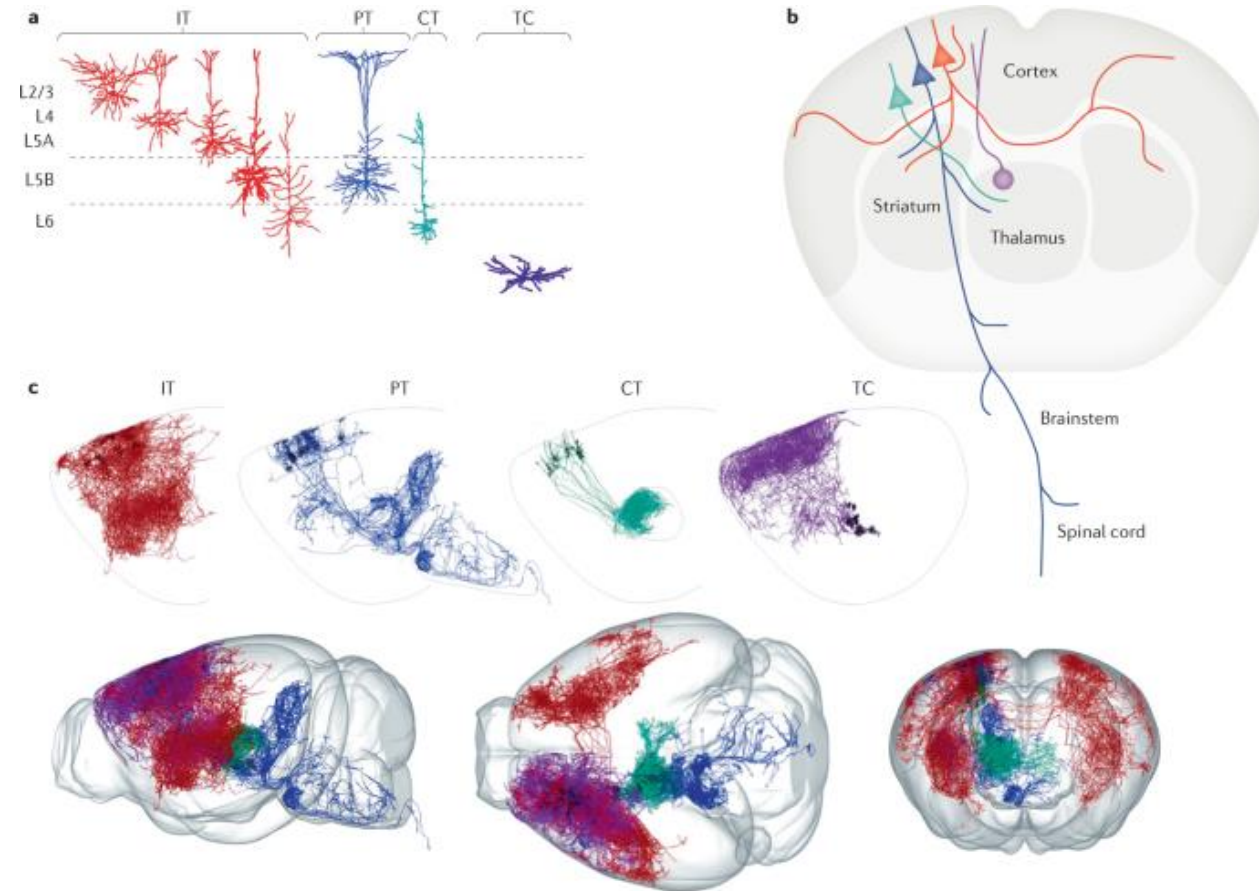


“neuroscience can provide validation of AI techniques that already exist. If a known algorithm is subsequently found to be implemented in the brain, then that is strong support for its plausibility as an integral component of an overall general intelligence system”

# Neural circuits are much more complex than modern AI systems ...



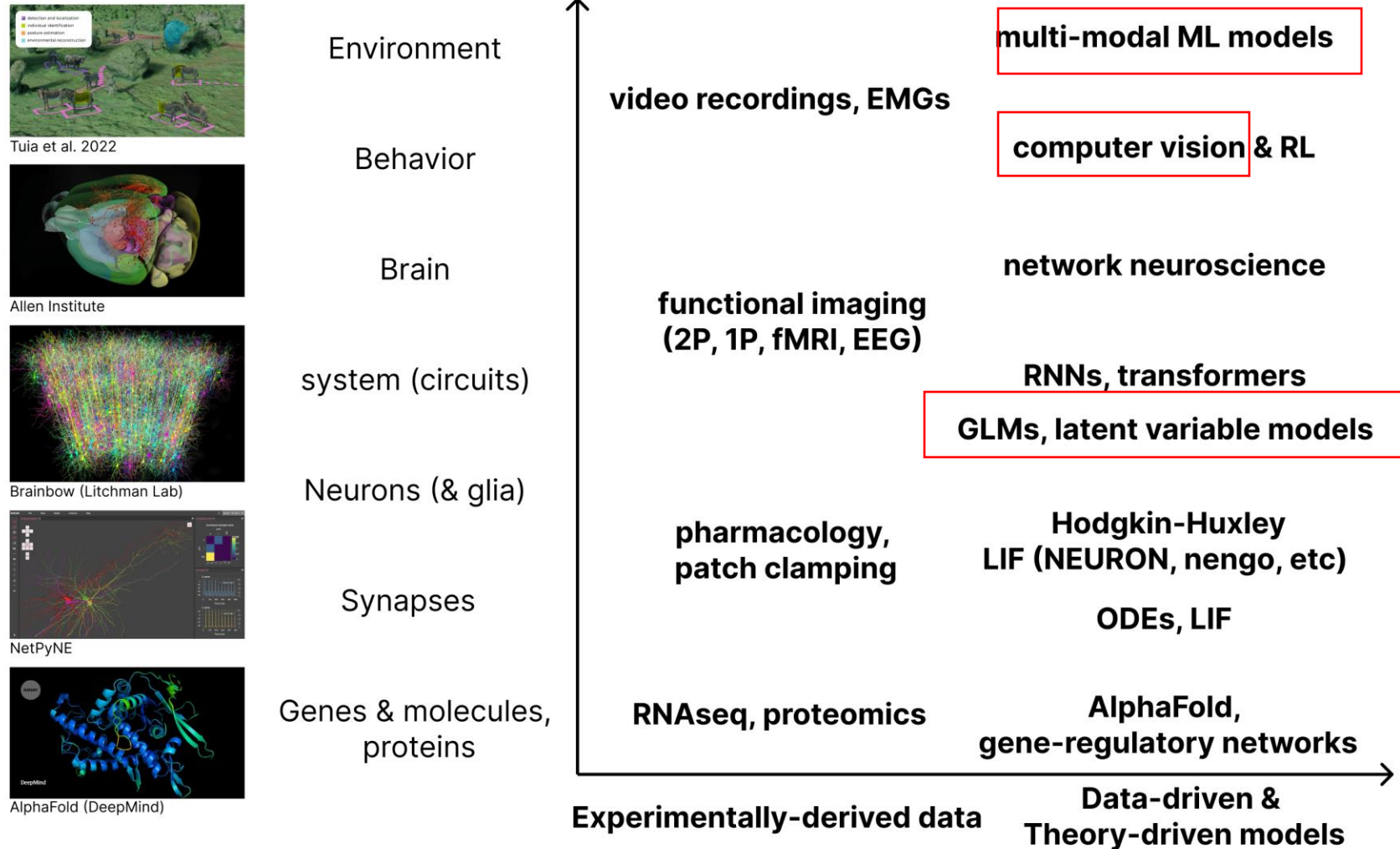
Felleman and Van Essen *Cerebral Cortex* 1991



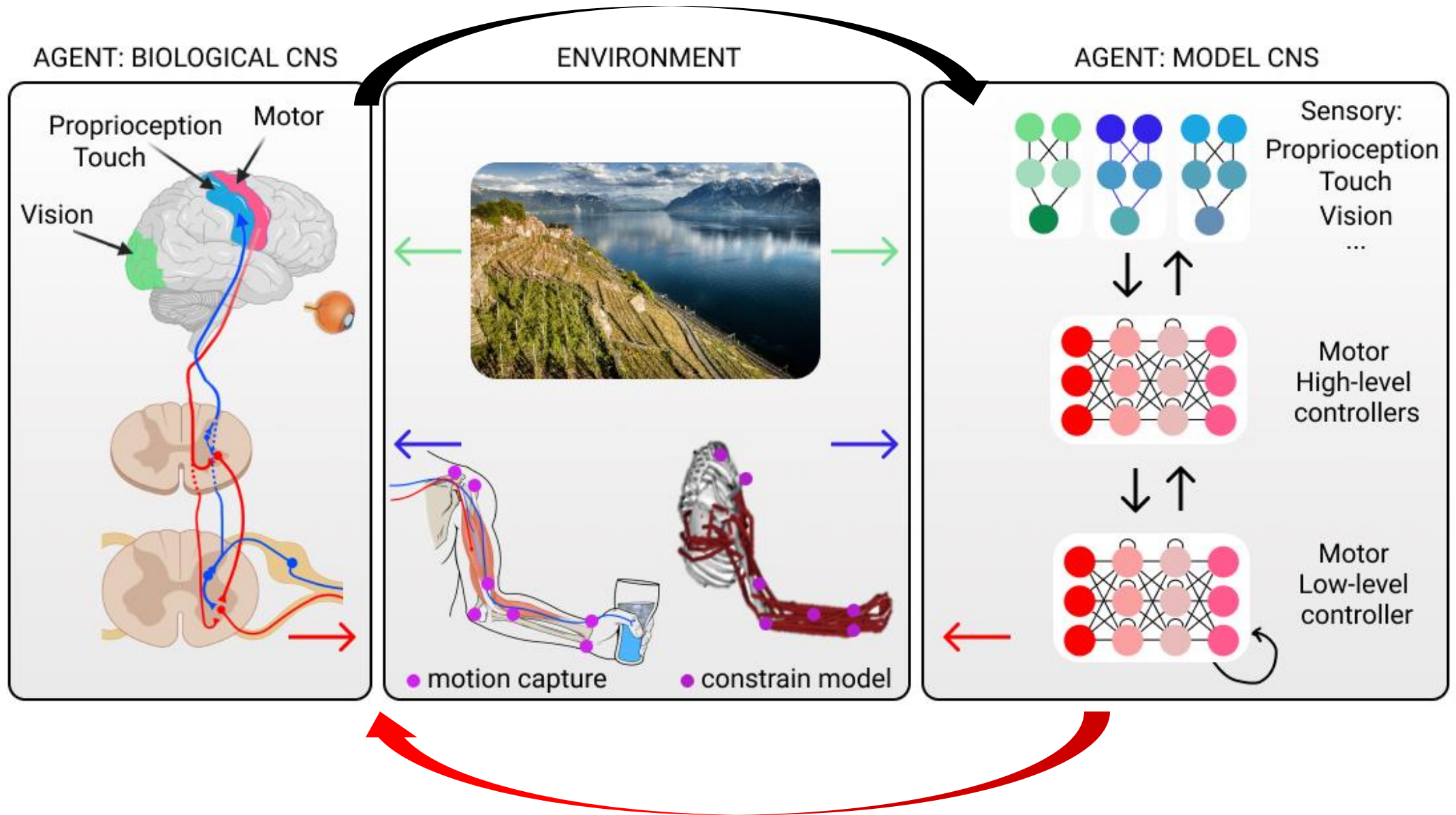
Shepherd and Yamawaki *Nature review neuroscience* 2021



# Previously we covered (some) tools for measuring and modeling behavioral and neural data with data-driven approaches ...

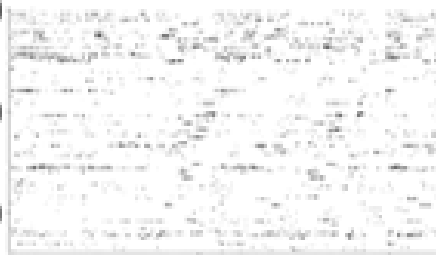


# Data-driven and Task-driven modeling for understanding BI

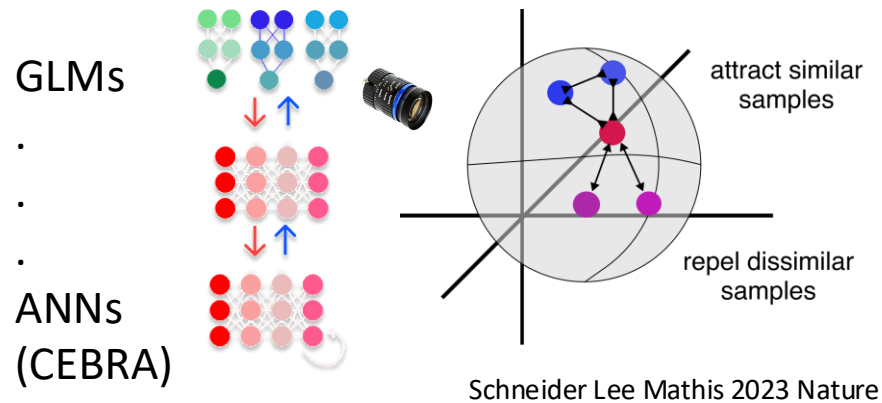


# Data-driven modeling

GLMs, PCA, Sussillo et al. 2015 Nat Neuro  
State-space models, ...



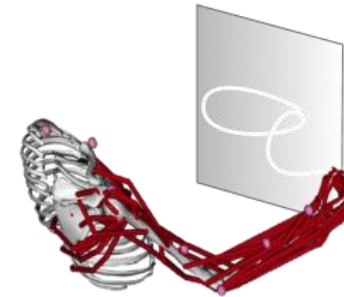
Record from neural data  
during a behavioral task



Joint models that describe  
neural variance & representations

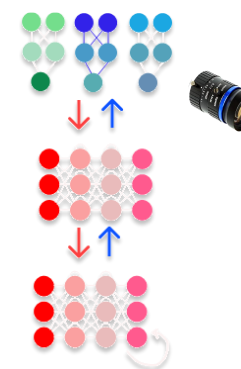
# Task-driven modelling

Yamins et al. PNAS 2014, Kell et al. 2018 Neuron,  
Banino et al. 2018 Nature ....

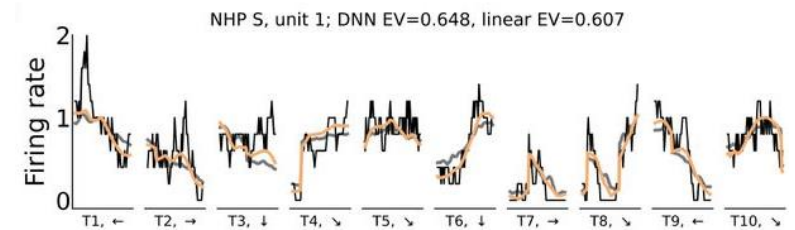


Constrain ANN based on  
behavioral task to test  
hypotheses about a system

Sandbrink et al. 2023 eLife



**Data**  
**Task-driven models (hand position and velocity task)**  
**Linear model**



Marin Vargas et al. 2024 Cell

NN models that describe  
neural variance & computationally  
constrain system

# Data-driven modeling

“If a new facet of biological computation found to be critical to supporting a cognitive function, then we would consider it an excellent candidate for incorporation into artificial systems”

# Task-driven modelling

“neuroscience can provide validation of AI techniques that already exist. If a known algorithm is subsequently found to be implemented in the brain, then that is strong support for its plausibility as an integral component of an overall general intelligence system”



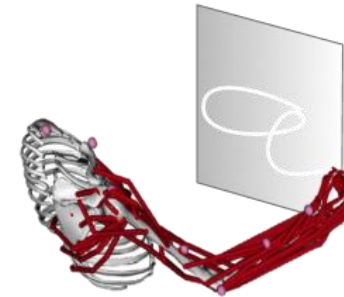


# Task-driven modelling

Yamins et al. PNAS 2014, Sussillo et al. 2015 Nat Neuro, Kell et al. 2018 Neuron, Banino et al. 2018 Nature ....

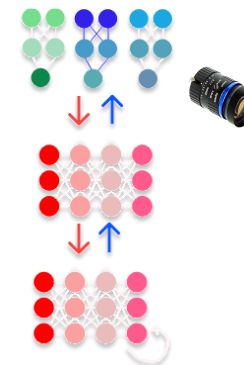
**how task-driven models  
can inform us about the  
computational goals of  
the brain**

***(which can lead to  
validations and/or new  
ideas for AI)***

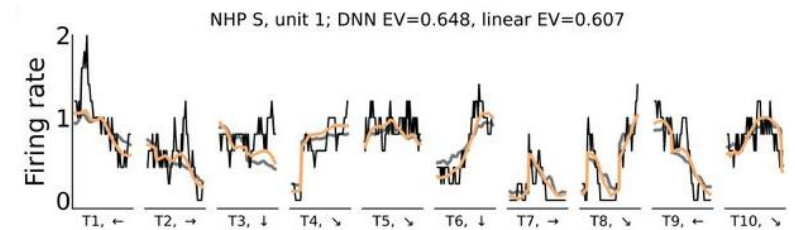


Constrain ANN based on  
behavioral task to test  
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Sandbrink et al. 2023 eLife



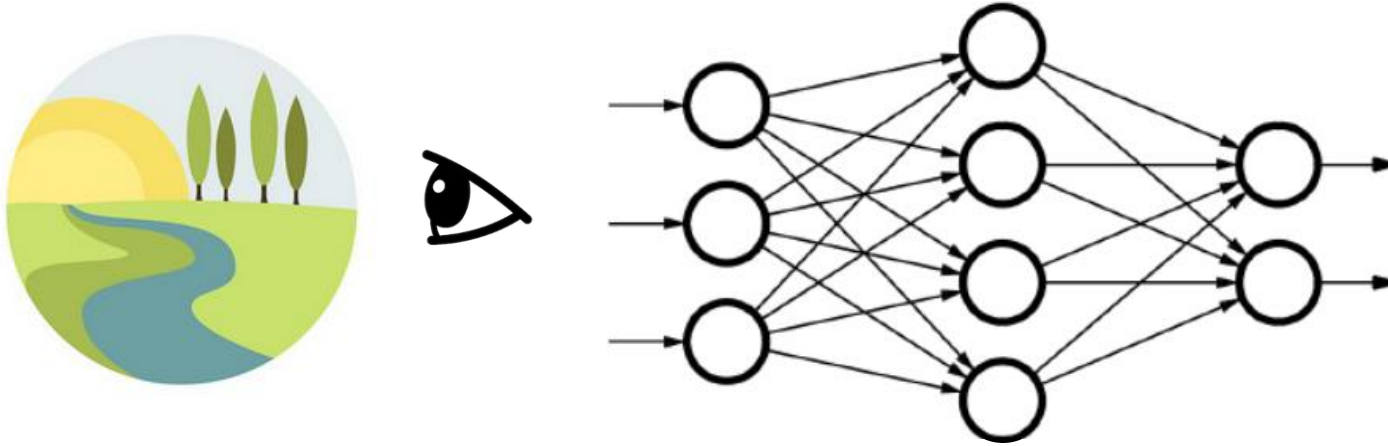
**Data**  
**Task-driven models (hand position and velocity task)**  
**Linear model**



Marin Vargas et al. 2024 Cell

NN models that describe  
neural variance & computationally  
constrain system

# Using deep neural networks as task-driven models of a system



cat



Vision: Yamins et al. (2014) .. Wang et al. (2025)



Audition: Kell et al. (2018)- speech recognition,  
speaker identification, natural sound  
identification



Barrel Cortex: Zhuang et al. (2017)



Cognition: Mante et al. (2013)



Proprioception: Sandbrink et al. (2023), Marin Vargas\*, Bisi\* et al. (2024)

# The goal: to build NN models that are constrained to goals of a neural system

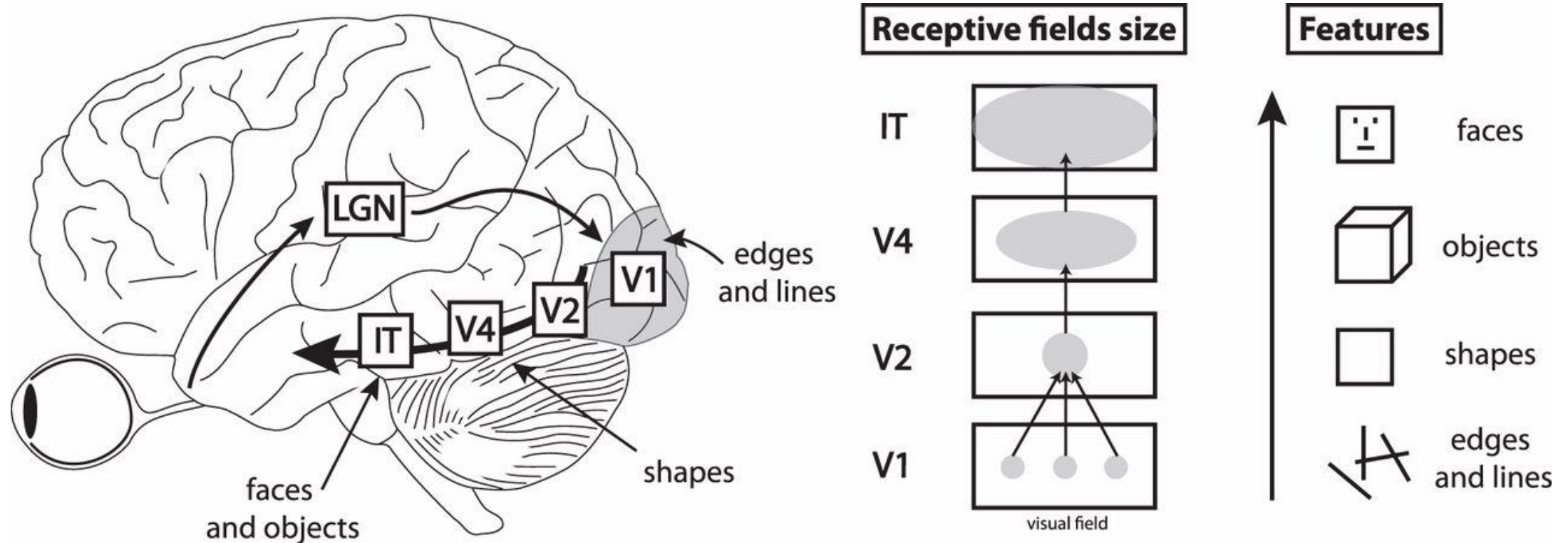
Machine learning	Neuroscience
Architecture	Circuits
Task / objective	Ecological niche
Dataset	Environment
Optimization method (learning rule)	Natural selection + synaptic plasticity



NN model



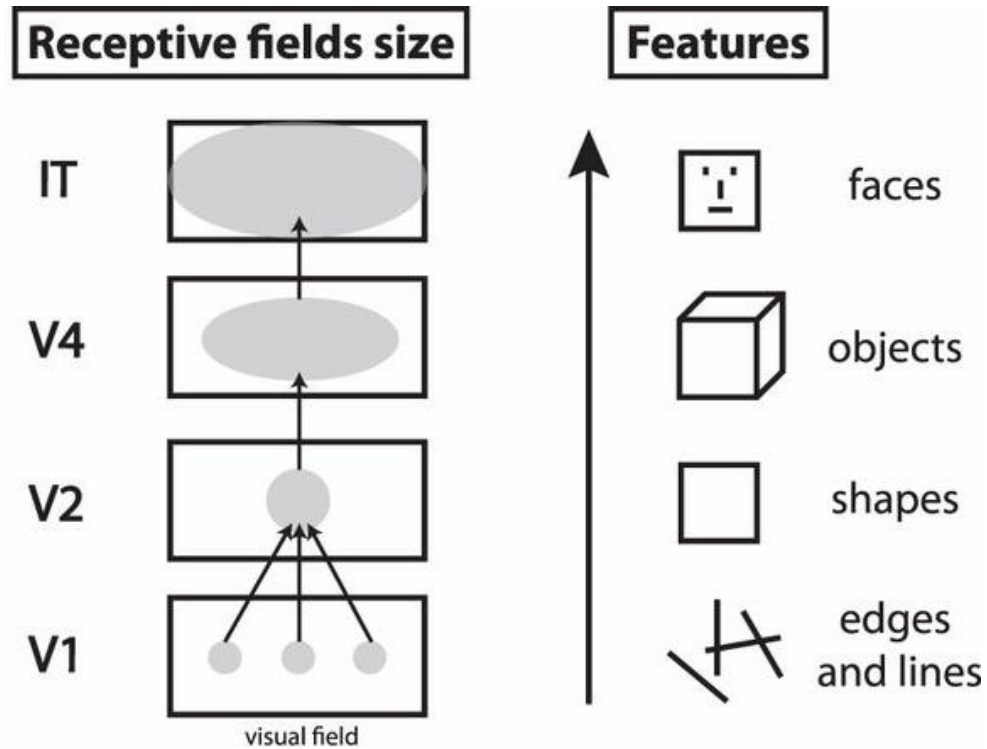
# Hierarchical visual processing



- V1 neurons are most sensitive to low-level features, such as edges and lines.
- In higher visual areas, like V4 and IT, receptive fields are larger, and neurons are sensitive to complex features, such as shapes and objects.
- Responses of high-level neurons are fully determined by the neural firing of lower-level neurons. For example, the neural firing to a square is determined by the neural firing for two vertical and two horizontal lines.



# IT neurons are nonlinear



From: When crowding of crowding leads to uncrowding  
Journal of Vision. 2013;13(13):10. doi:10.1167/13.13.10

## The Code for Facial Identity in the Primate Brain

Le Chang<sup>1,\*</sup> and Doris Y. Tsao<sup>1,2,3,\*</sup>

<sup>1</sup>Division of Biology and Biological Engineering, Computation and Neural Systems, Caltech, Pasadena, CA 91125, USA

<sup>2</sup>Howard Hughes Medical Institute, Pasadena, CA 91125, USA

<sup>3</sup>Lead Contact

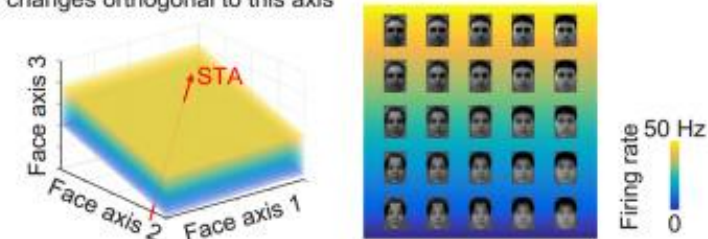
\*Correspondence: [lechang@caltech.edu](mailto:lechang@caltech.edu) (L.C.), [dortsao@caltech.edu](mailto:dortsao@caltech.edu) (D.Y.T.)

<http://dx.doi.org/10.1016/j.cell.2017.05.011>

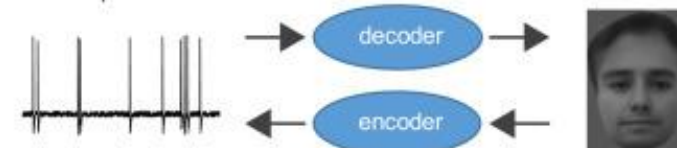
1. We recorded responses to parameterized faces from macaque face patches



2. We found that single cells are tuned to single face axes, and are blind to changes orthogonal to this axis

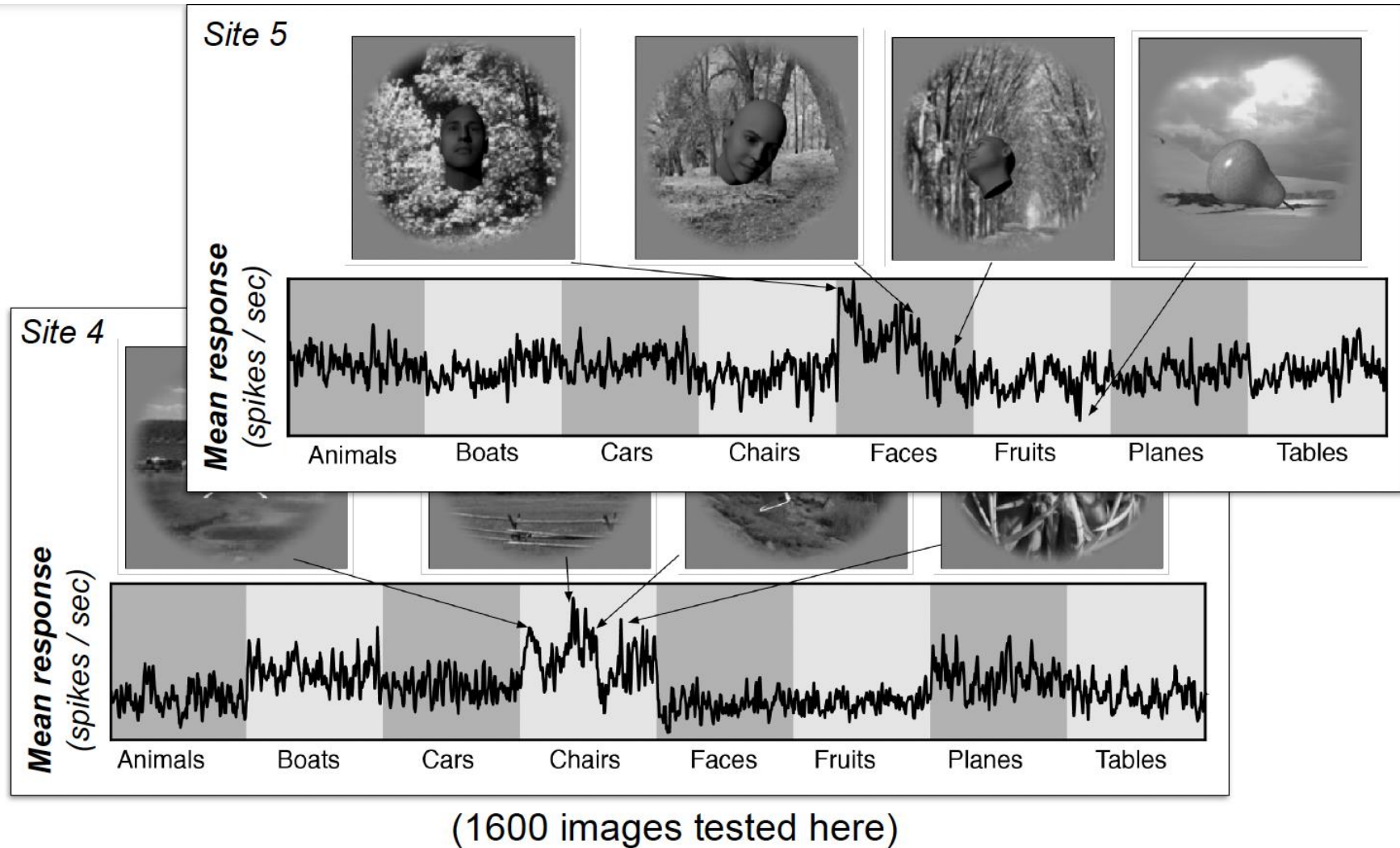


3. We found that an axis model allows precise encoding and decoding of neural responses

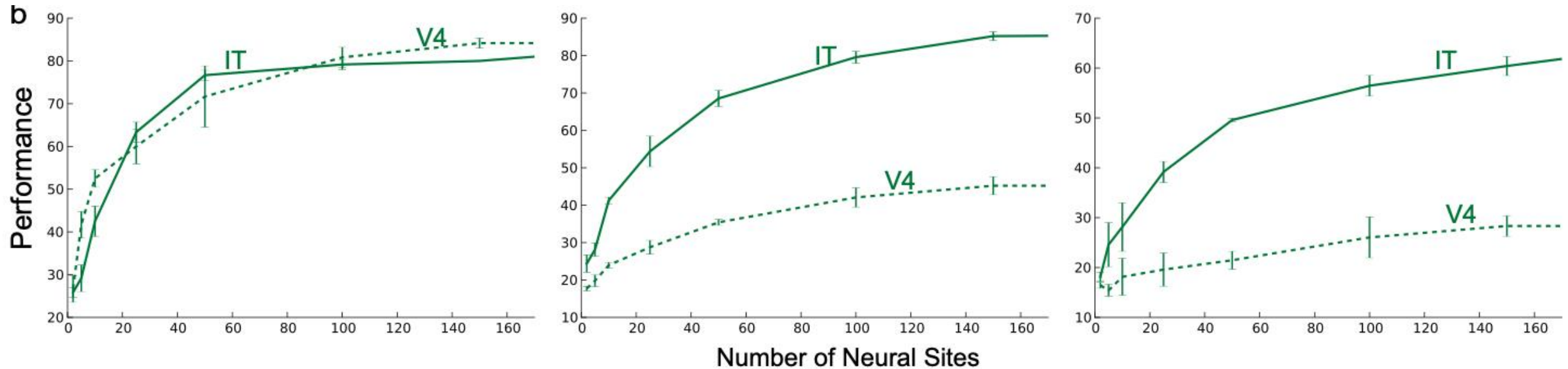
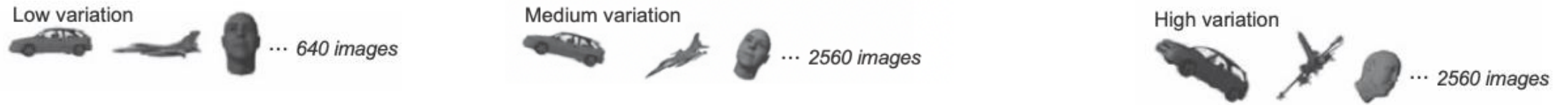


# Example higher-order visual cortex responses

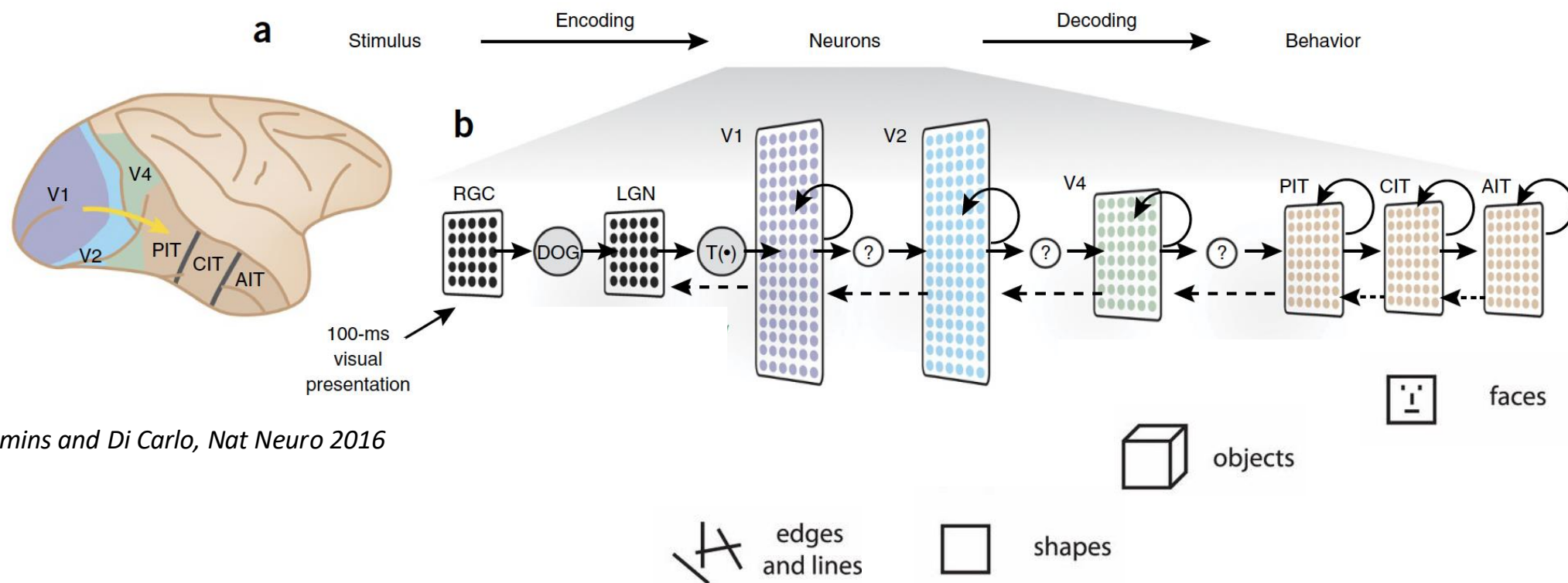
Examples of IT neuronal spiking responses



# Decoding object identity from neural data



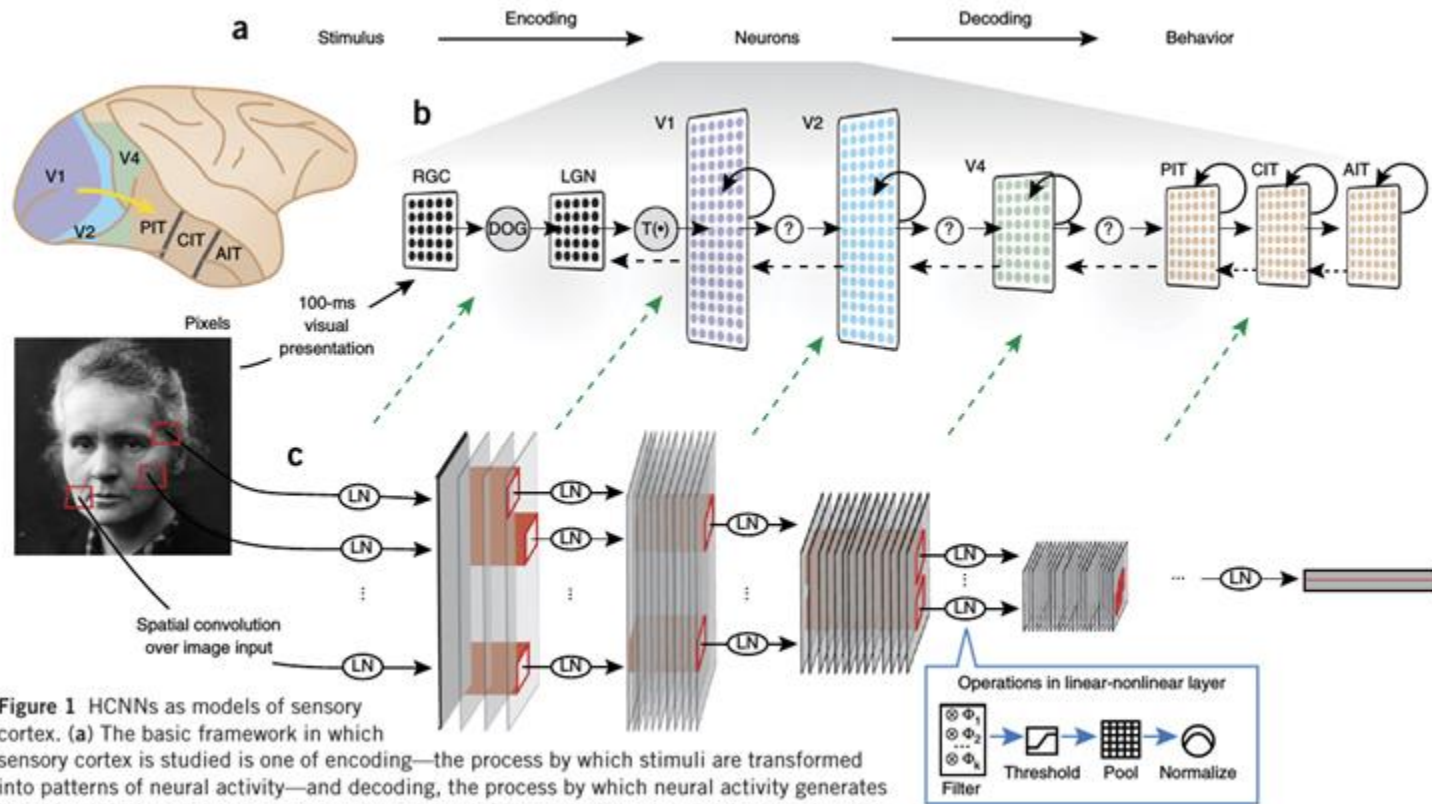
# Core-object recognition and the visual pathway



*Yamins and Di Carlo, Nat Neuro 2016*



# Building models of visual pathway: what is the computational goal?



**Figure 1** HCNNs as models of sensory cortex. (a) The basic framework in which sensory cortex is studied is one of encoding—the process by which stimuli are transformed into patterns of neural activity—and decoding, the process by which neural activity generates behavior. HCNNs have been used to make models of the encoding step; that is, they describe

Task information consistency

Single-unit response predictivity

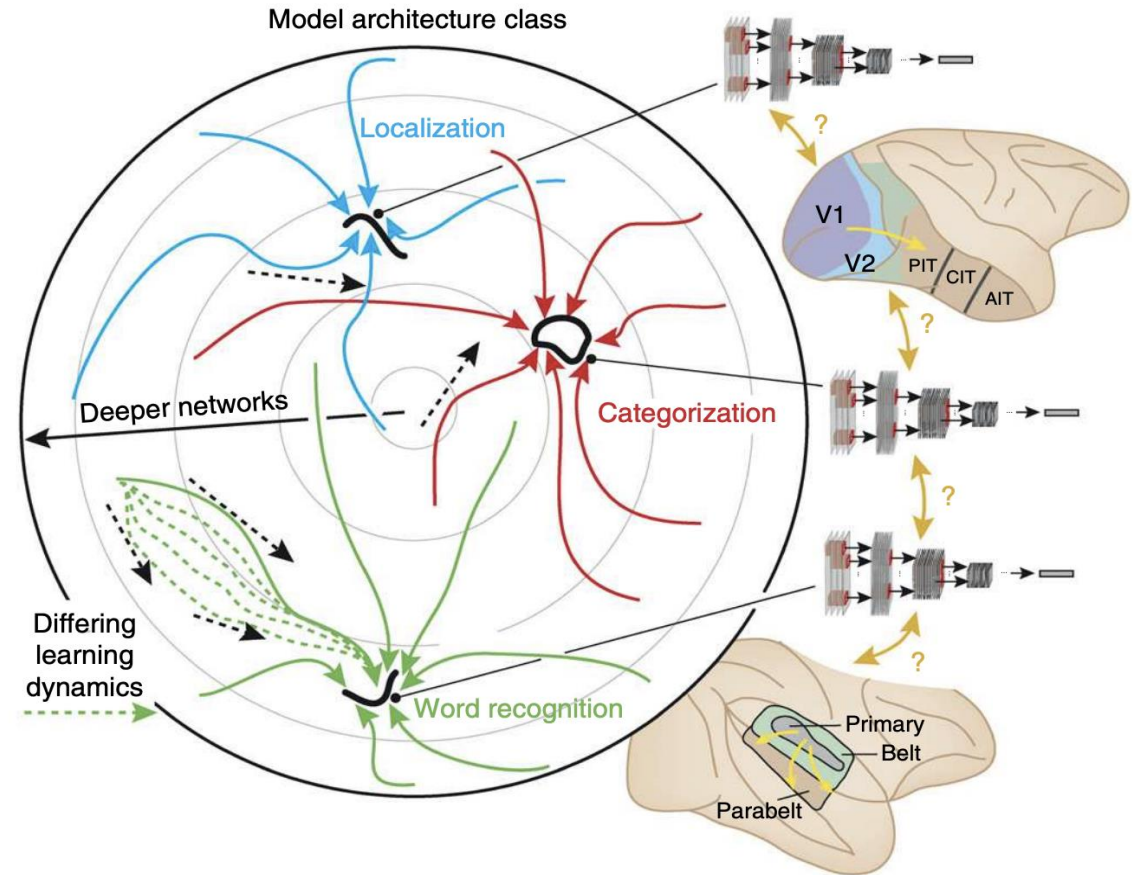
Population representational similarity

Yamins & DiCarlo Nature Neuroscience 2016

# Building models of visual pathway: the ingredients

Task-driven deep neural network models are built from three basic components:

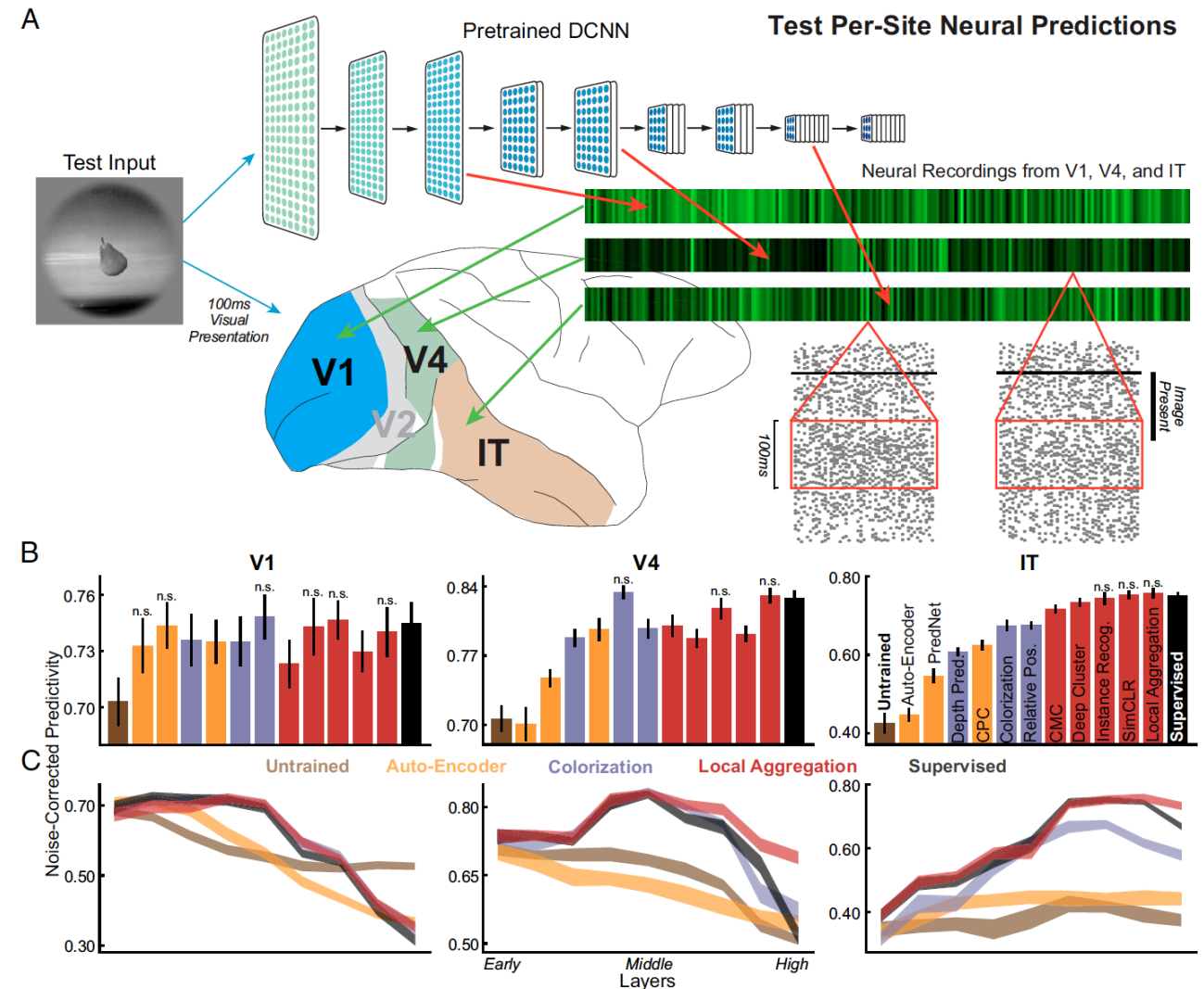
1. **model architecture class** from which the system is built, formalizing knowledge about the brain's anatomical and functional connectivity;
2. a **behavioral goal** that the system must accomplish, such as object categorization; and
3. a **learning rule** that optimizes parameters within the model class to achieve the behavioral goal.



Yamins & DiCarlo (2016)

# Learning, architecture search, and model comparison across visual areas

- Recordings from across the visual hierarchy
- Trained models outperform untrained models
- Supervised ImageNet models do very well, and so do unsupervised models...
- Early-Middle layers best predict V1, middle layer predict V4 and High layers best predict IT



# Representational similarity analysis

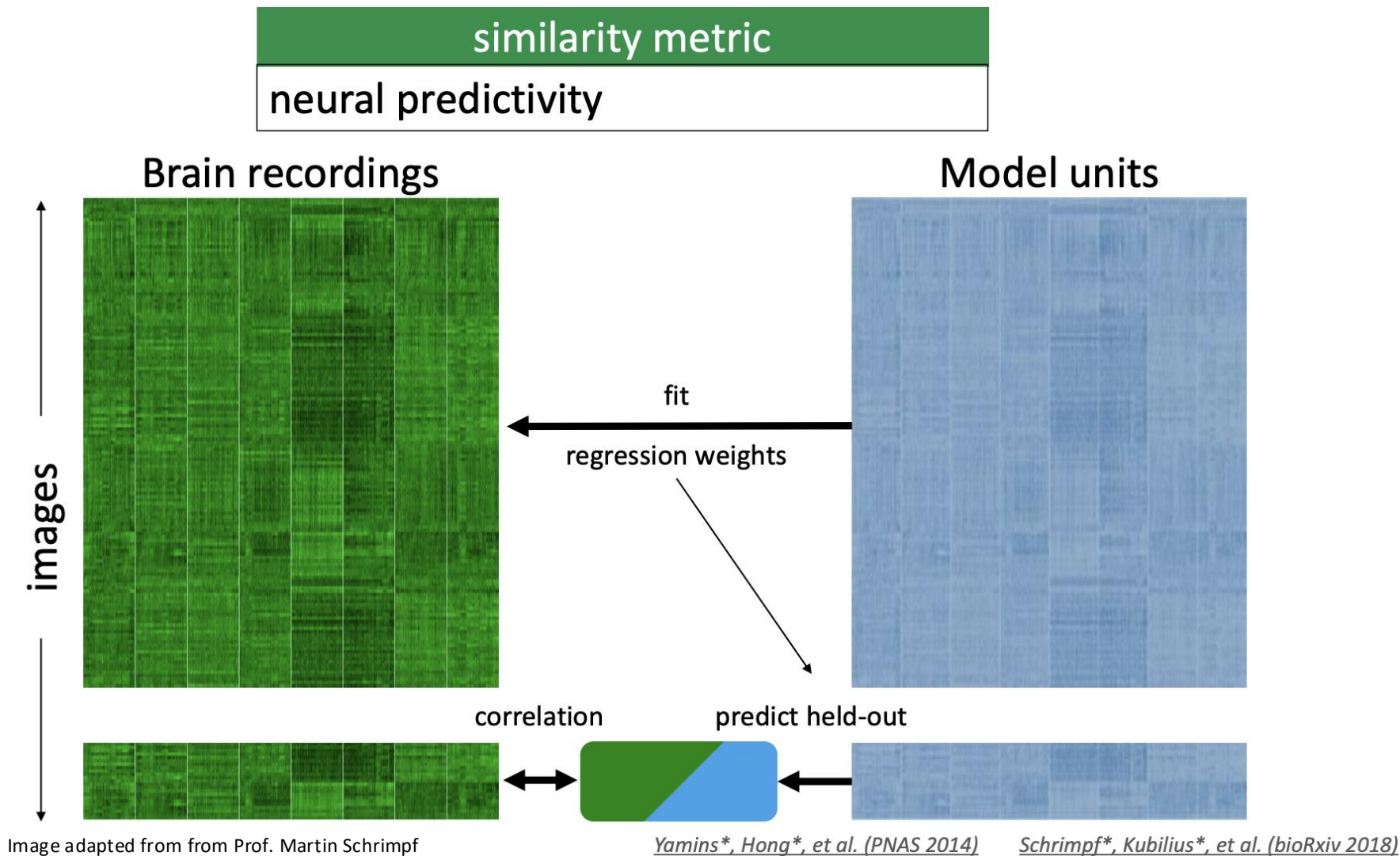


Image adapted from from Prof. Martin Schrimpf

*Yamins\*, Hong\*, et al. (PNAS 2014)*

*Schrimpf\*, Kubilius\*, et al. (bioRxiv 2018)*

- Representational Similarity Analysis (RSA) is a method to compare neural or model representations by **computing pairwise dissimilarities between activity patterns** (e.g., fMRI, neural data, or model activations) and comparing the resulting *representational dissimilarity matrices* (RDMs) across conditions
- Given  $n$  conditions with neural (or model) responses  $\mathbf{r}_1, \mathbf{r}_2, \dots, \mathbf{r}_n \in \mathbb{R}^d$ , RSA computes a Representational Dissimilarity Matrix (RDM)  $D \in \mathbb{R}^{n \times n}$  where:

$$D_{ij} = 1 - \text{corr}(\mathbf{r}_i, \mathbf{r}_j)$$

Commonly,  $\text{corr}(\cdot, \cdot)$  is Pearson or cosine correlation.



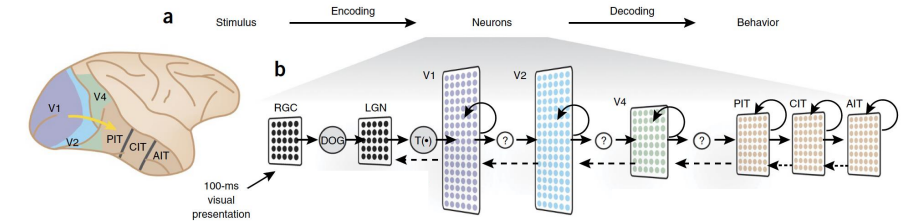
## Intermediate Take Homes:

- NN models can be trained on different visual tasks to make hypotheses about the goal of the visual system
- Better NN models at the categorization task predicted IT neurons better
- Task mattered more than architecture or depth of networks
- Three points to consider when comparing:

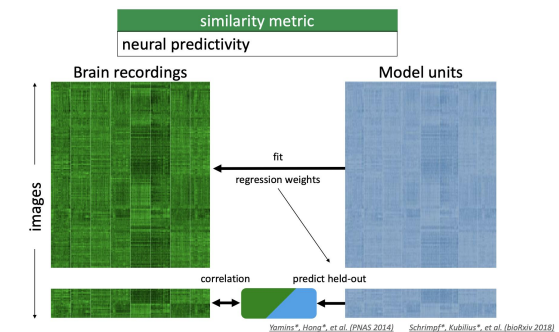
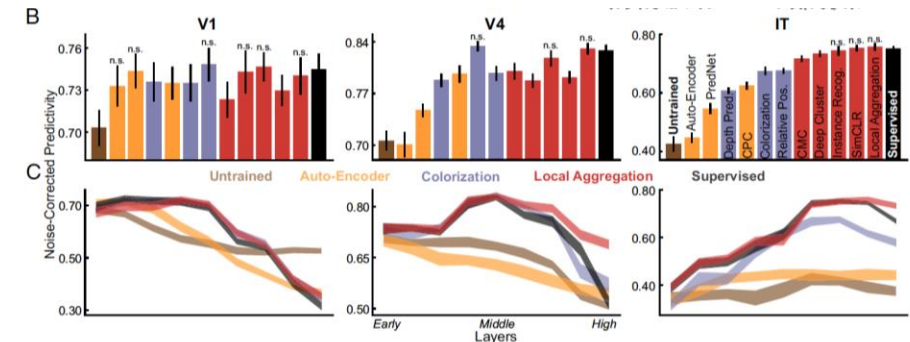
Task information consistency

Single-unit response predictivity

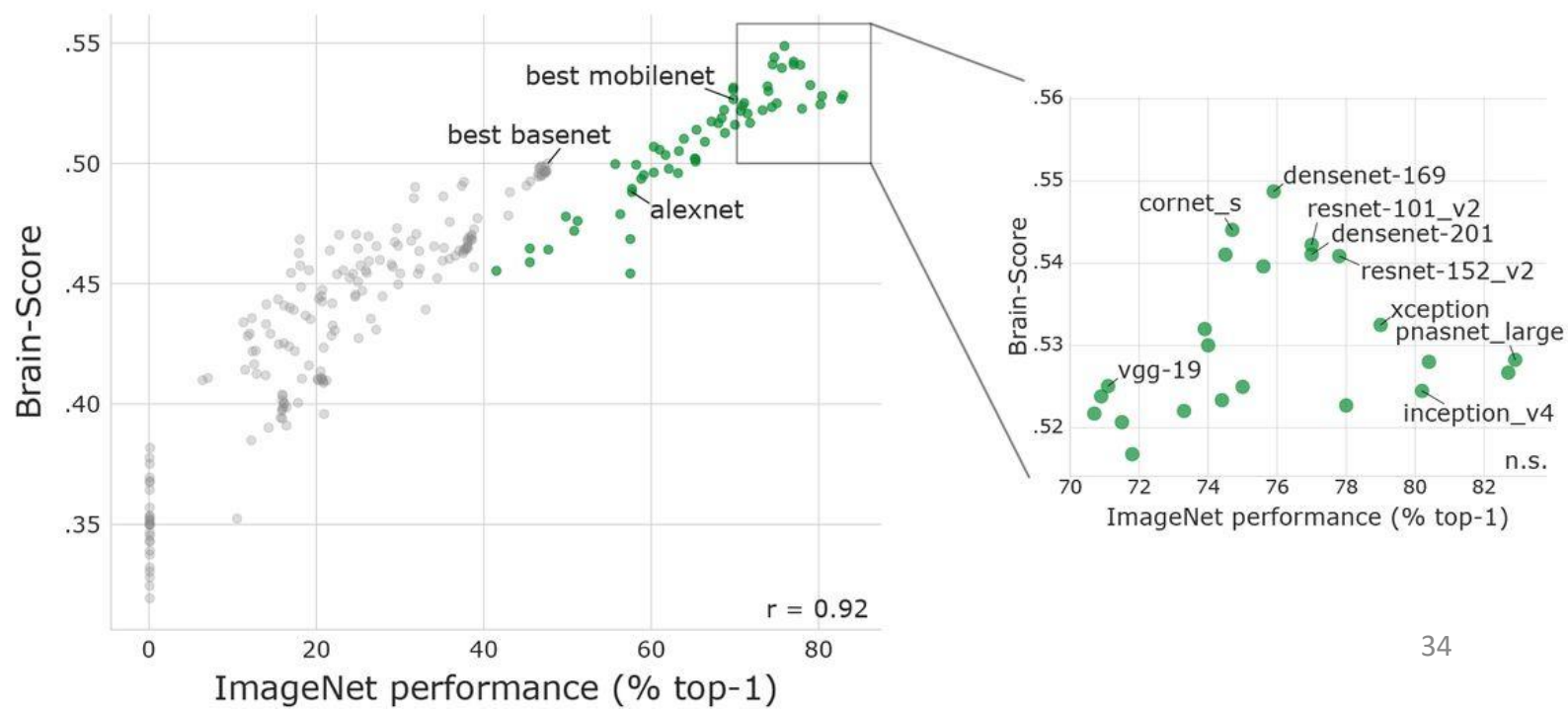
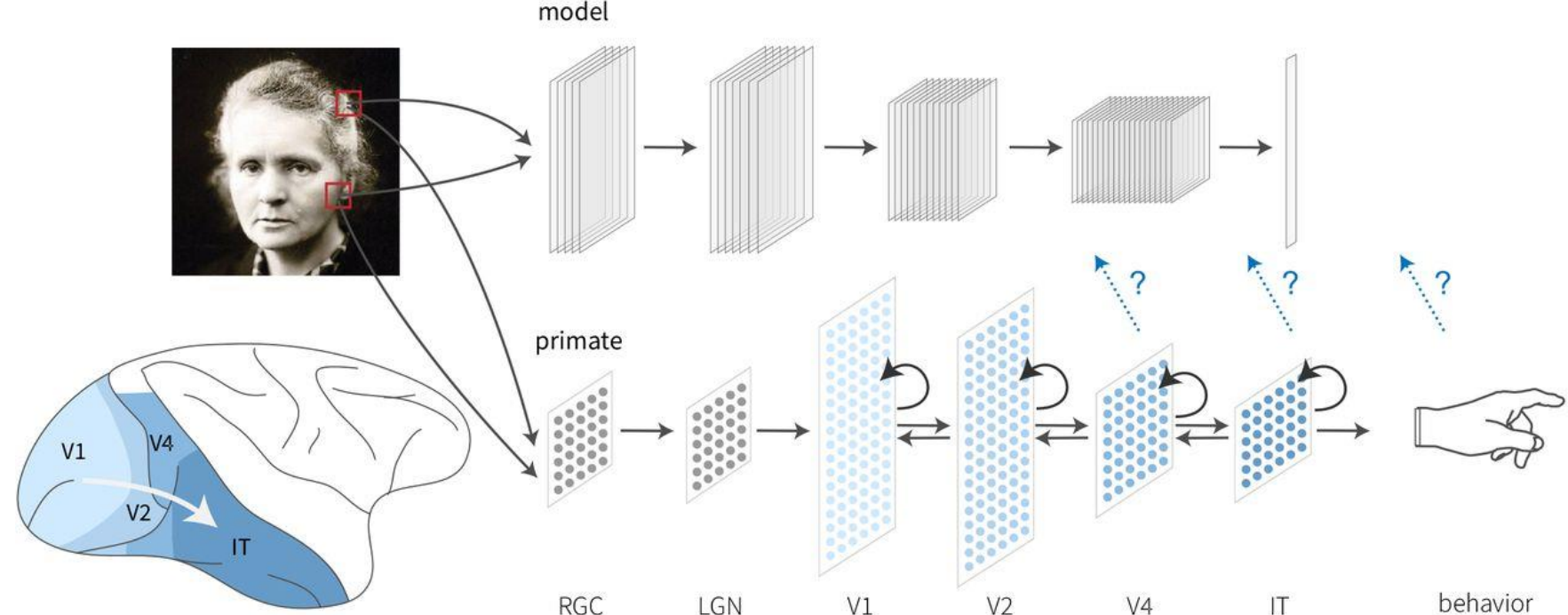
Population representational similarity



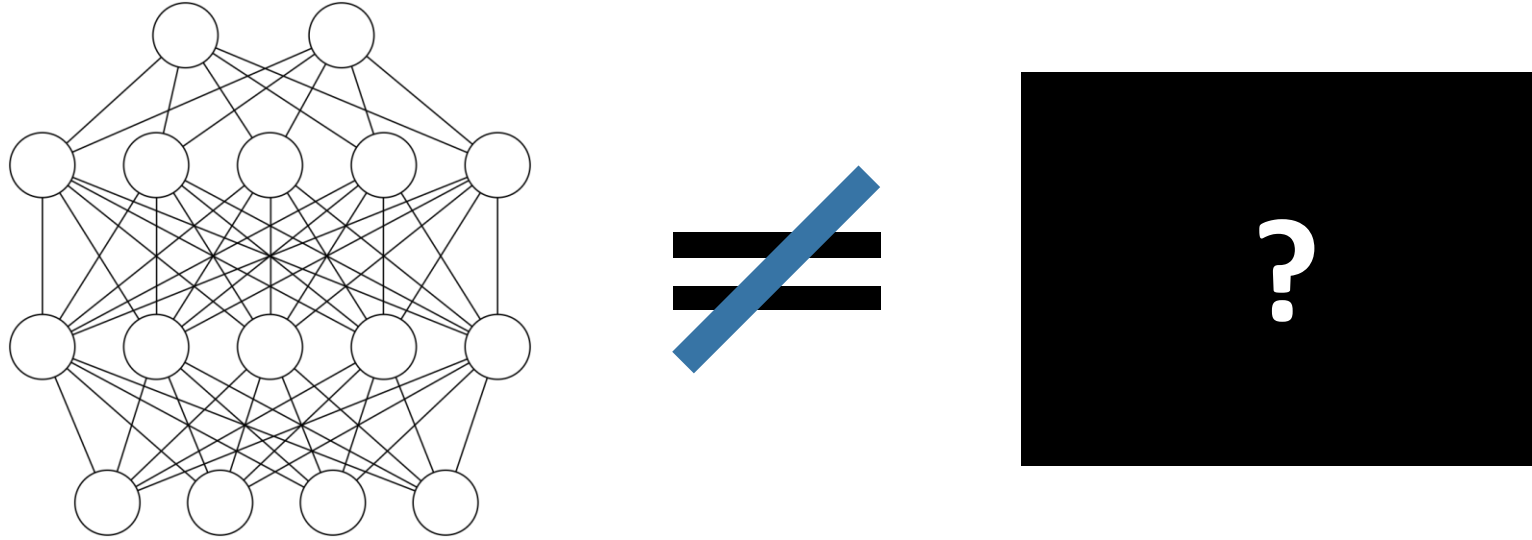
Yamins and Di Carlo, Nat Neuro 2016



## The hunt continues ...



# Deep Neural networks are not entirely a black box!



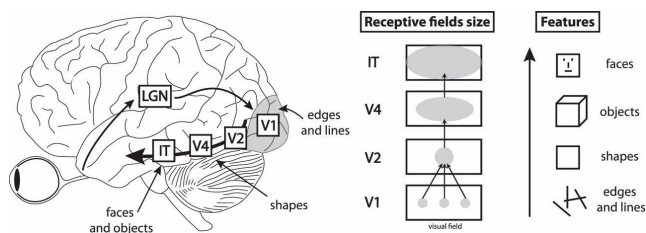
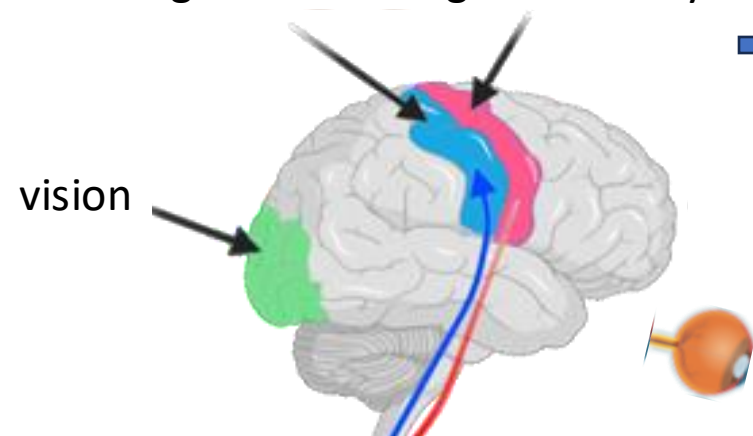
- can perform millions of *in silico* experiments
- derive experimentally testable predictions



# What other tasks? What other stimuli is the brain (visual) encoding?

Biological: recordings in visual system

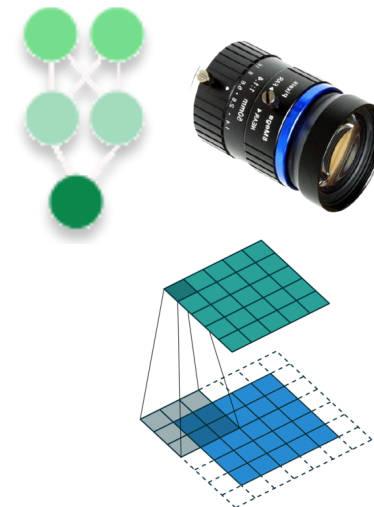
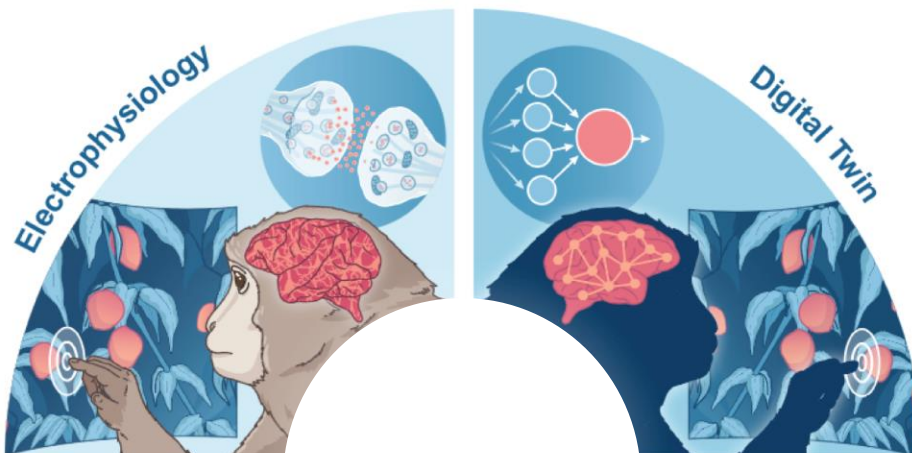
Building “digital twins”, NN models of the system



Hubel & Wiesel discoveries in cat V1  
inspired convolutional neural networks

We now know a lot more (faces,  
motion, value coding) but we  
never can give enough stimuli ....

**What would the ideal stimulus  
be for a given neuron?**

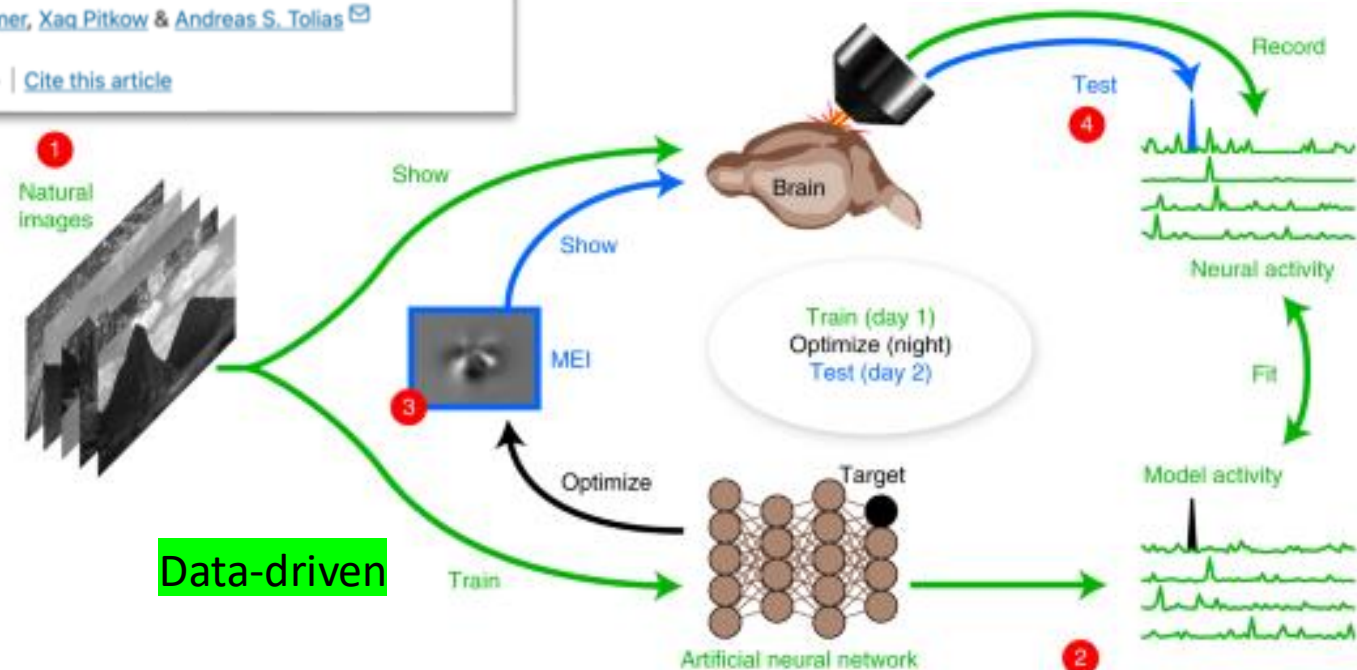
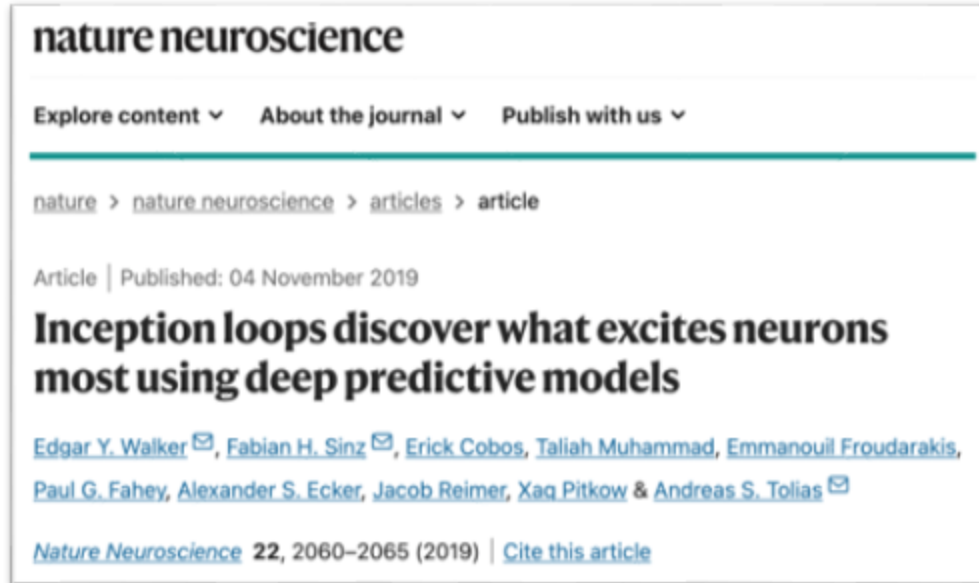


Can we use our NN to produce  
predictions of optimal stimuli?

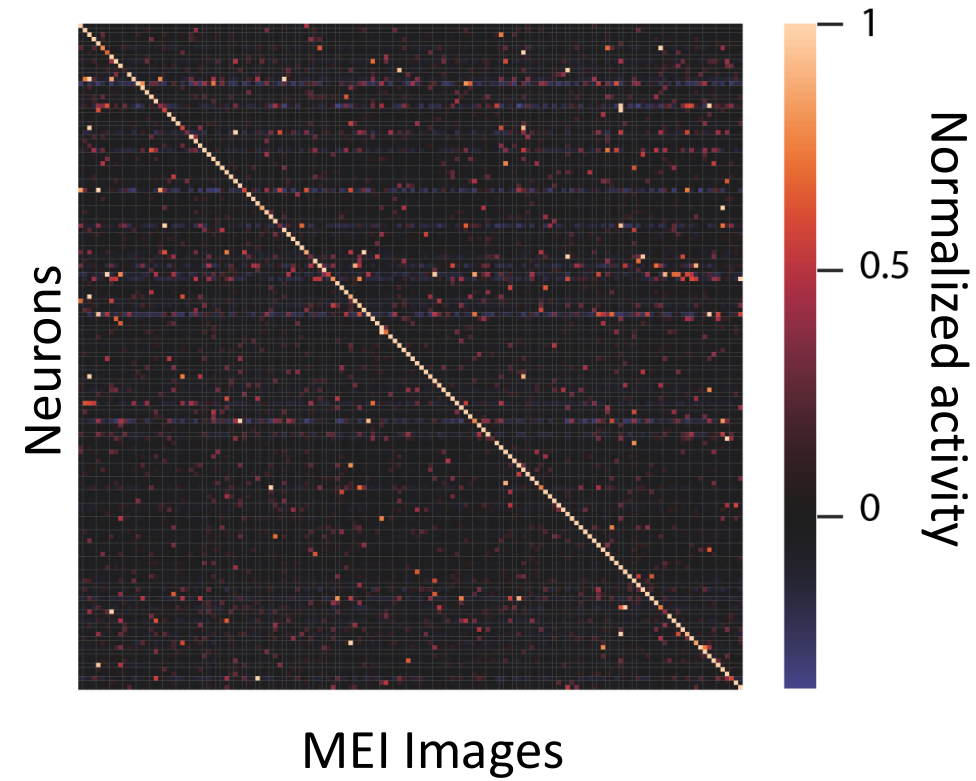
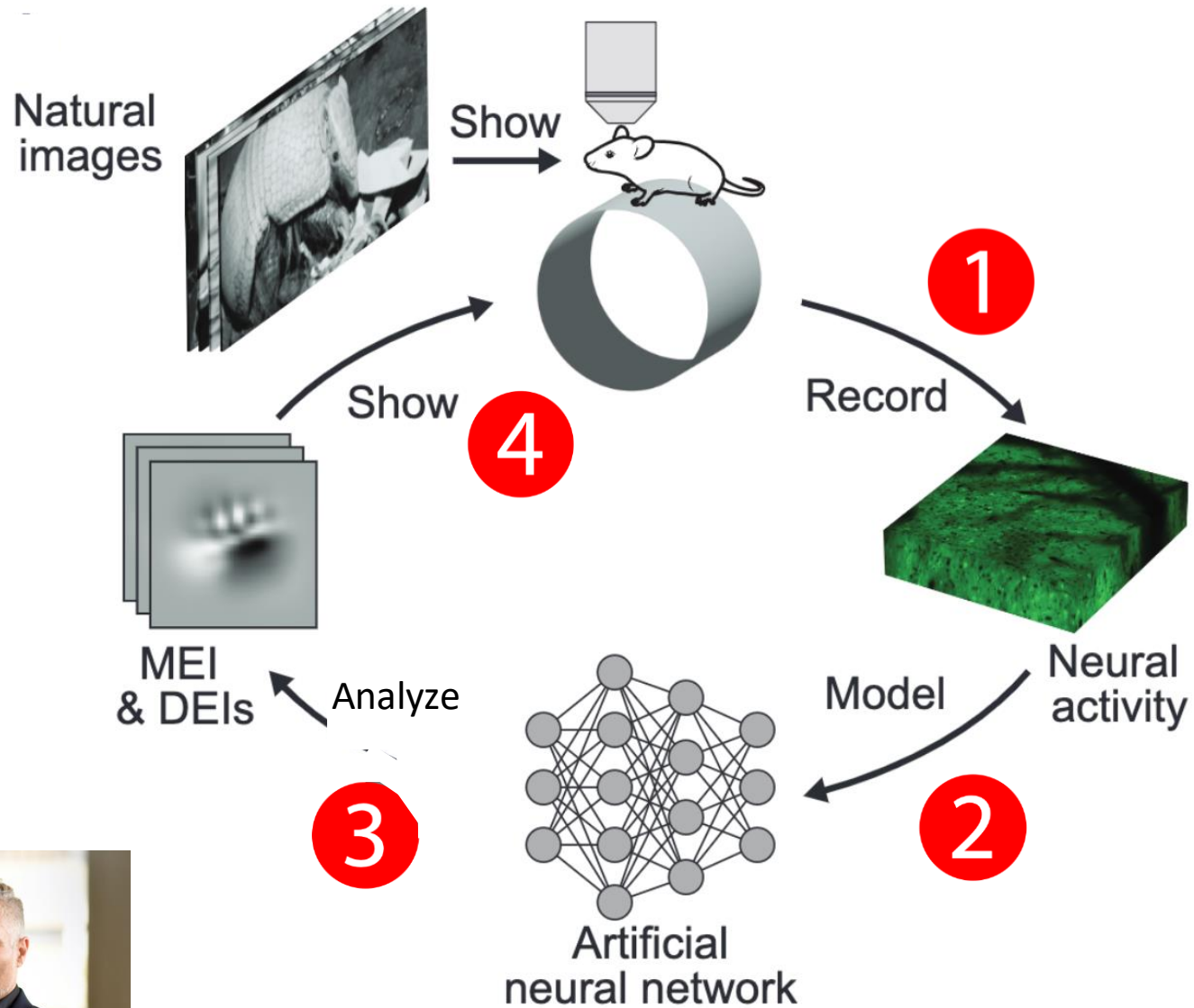
Can this help reveal a new  
computational principle, or  
validate a discovered rule?



# Paper reading: developing deep predictive models for causal testing!

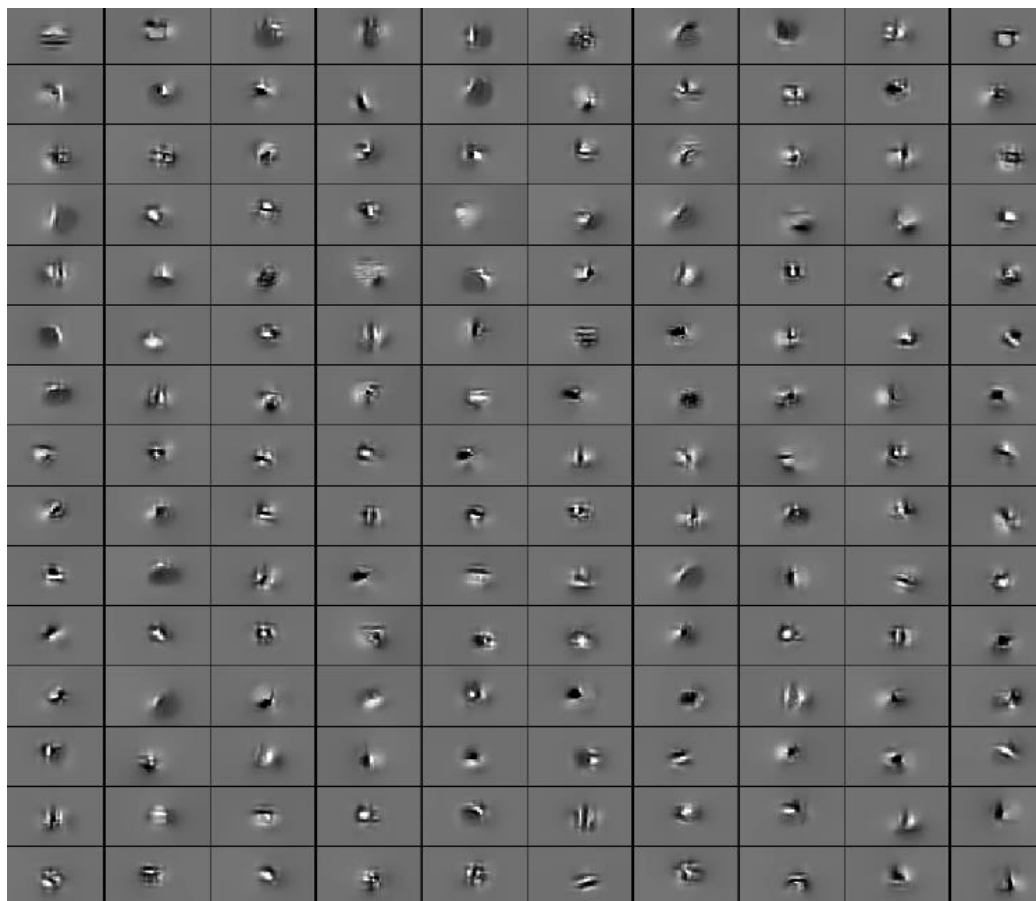


# In vivo verification



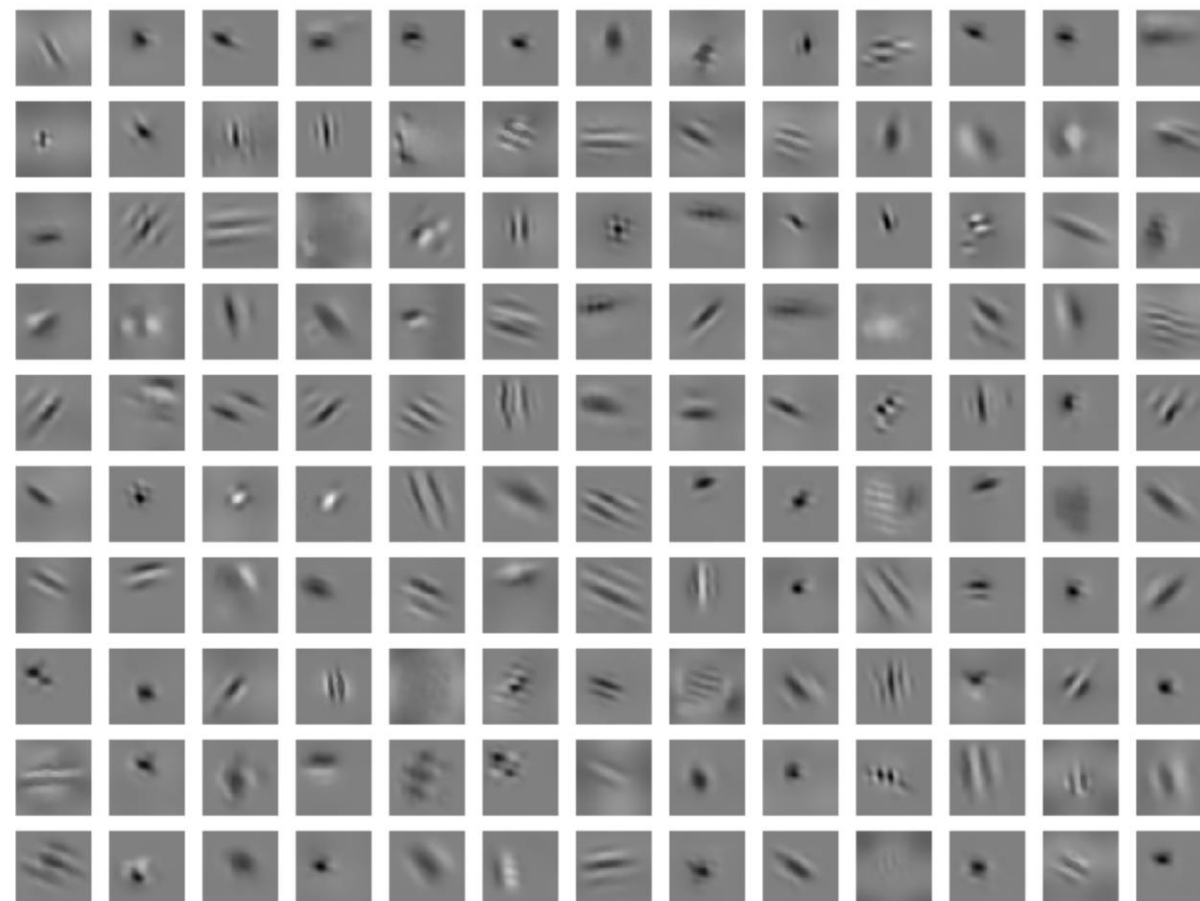
# What about MEIs in macaque V1?

## Mouse primary visual cortex



30 deg

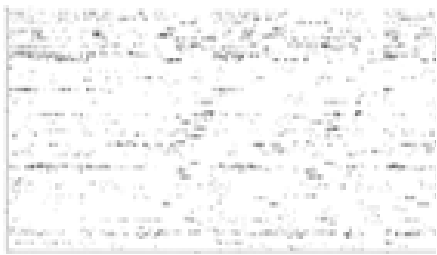
## Macaque primary visual cortex



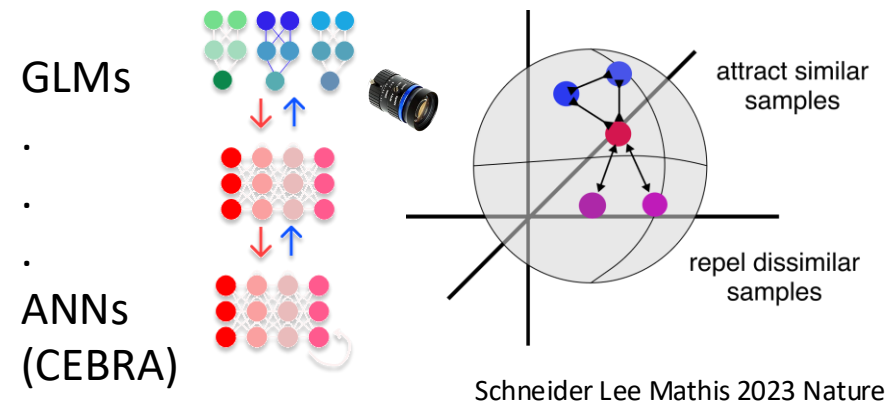
2 deg

# Data-driven modeling

GLMs, PCA, Sussillo et al. 2015 Nat Neuro  
State-space models, ...



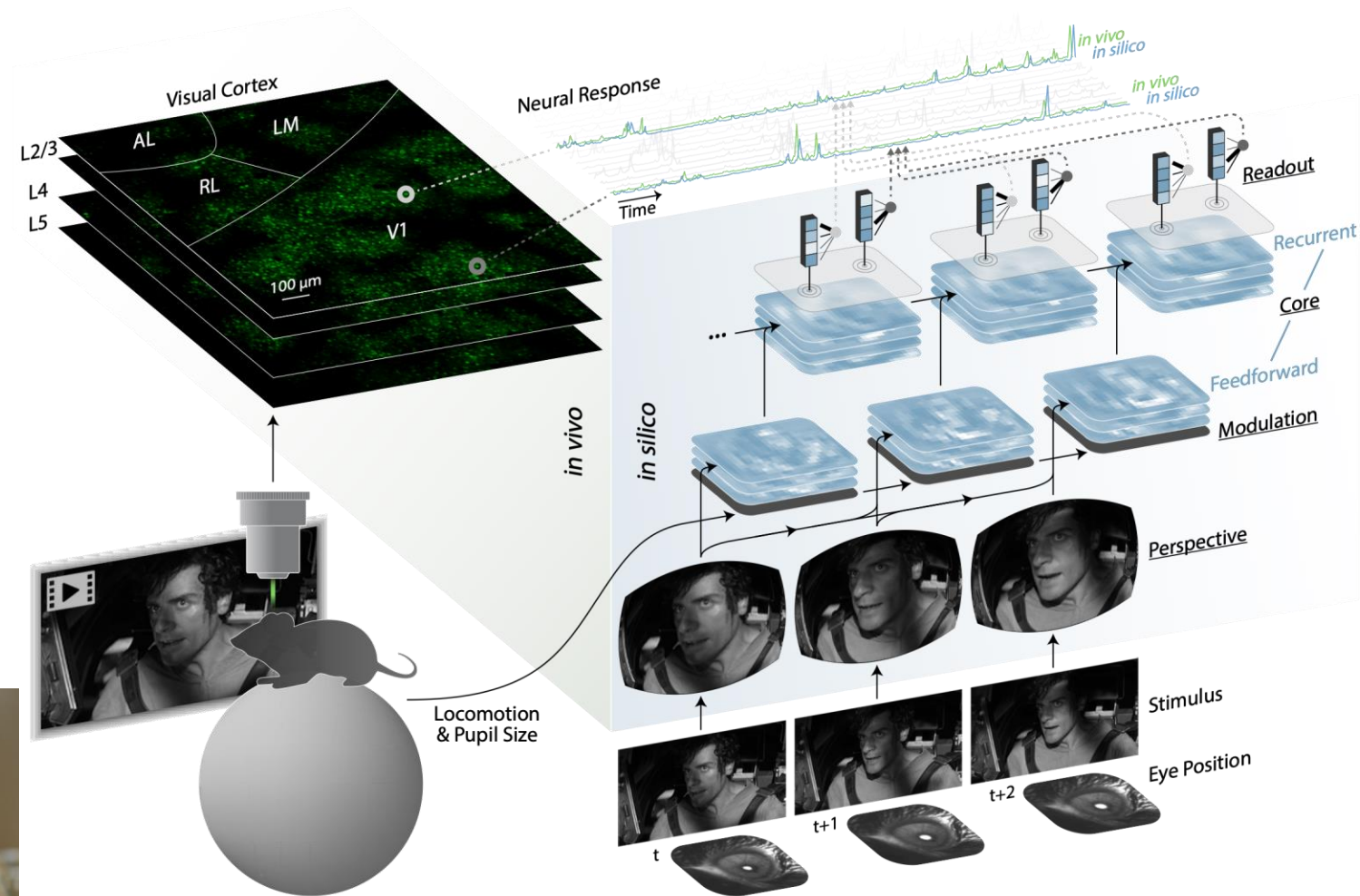
Record from neural data  
during a behavioral task



Joint models that describe  
neural variance & representations



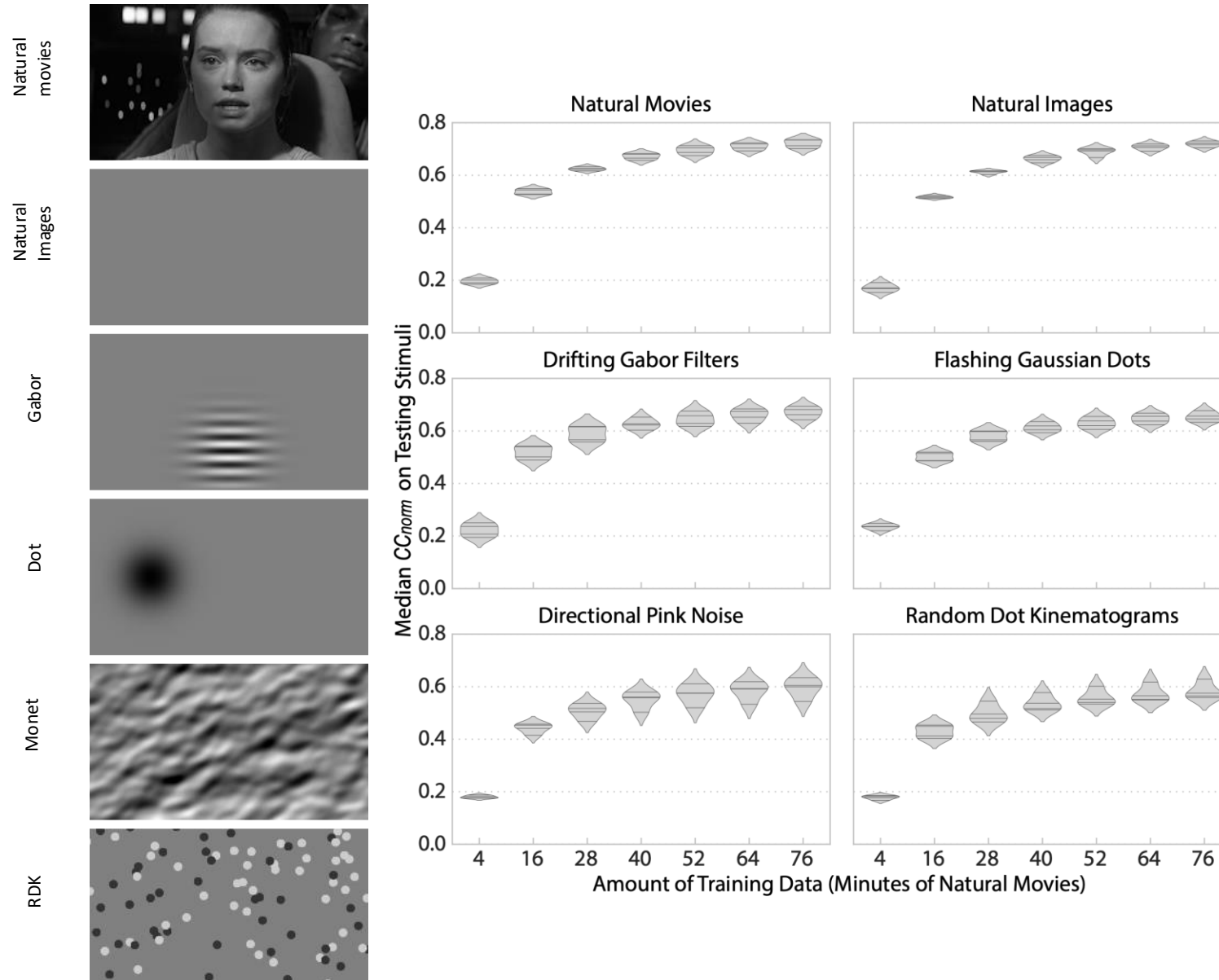
# Generalization to new neurons, mice, stimulus domains and morphological cell types



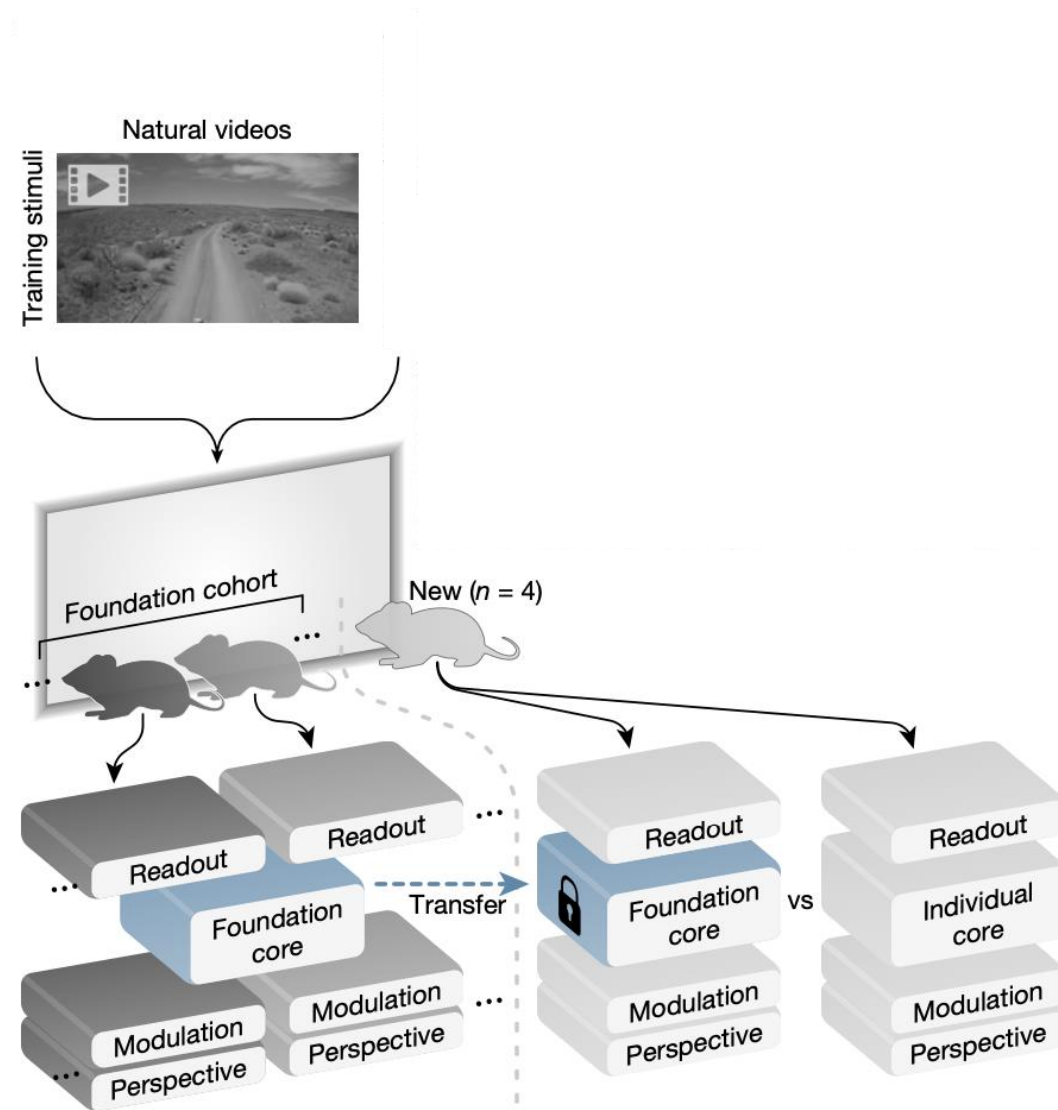
Eric Wang

Slide courtesy of Prof. Andreas Tolias

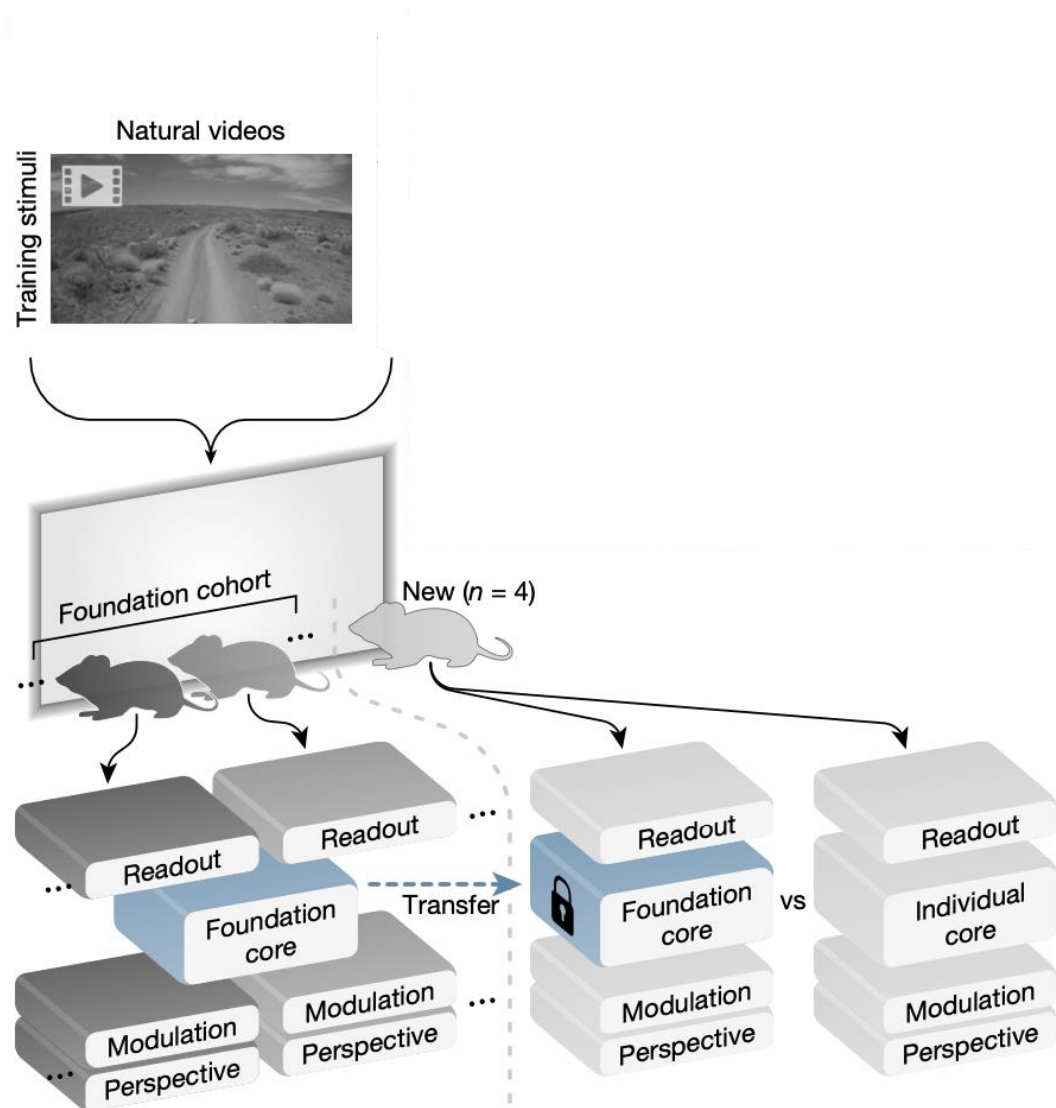
# Generalization to out-of-distribution stimuli



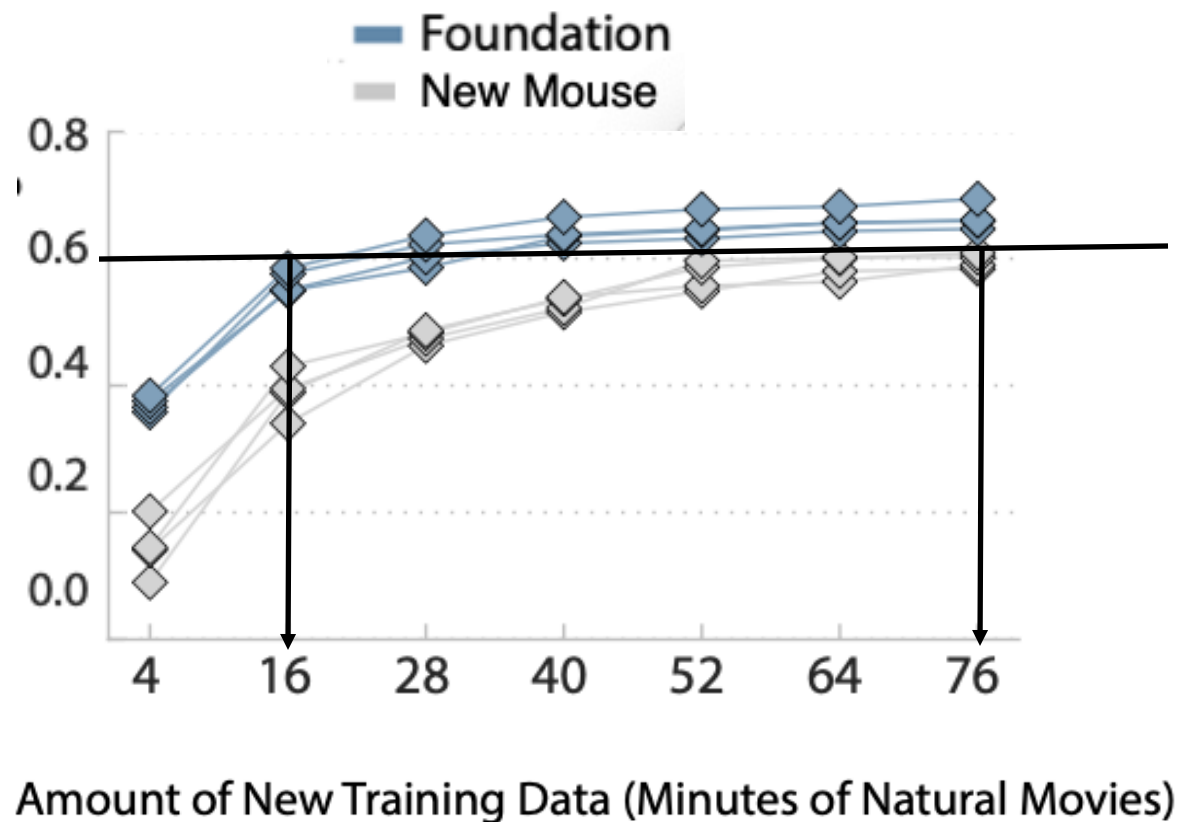
# Generalization to new neurons and mice



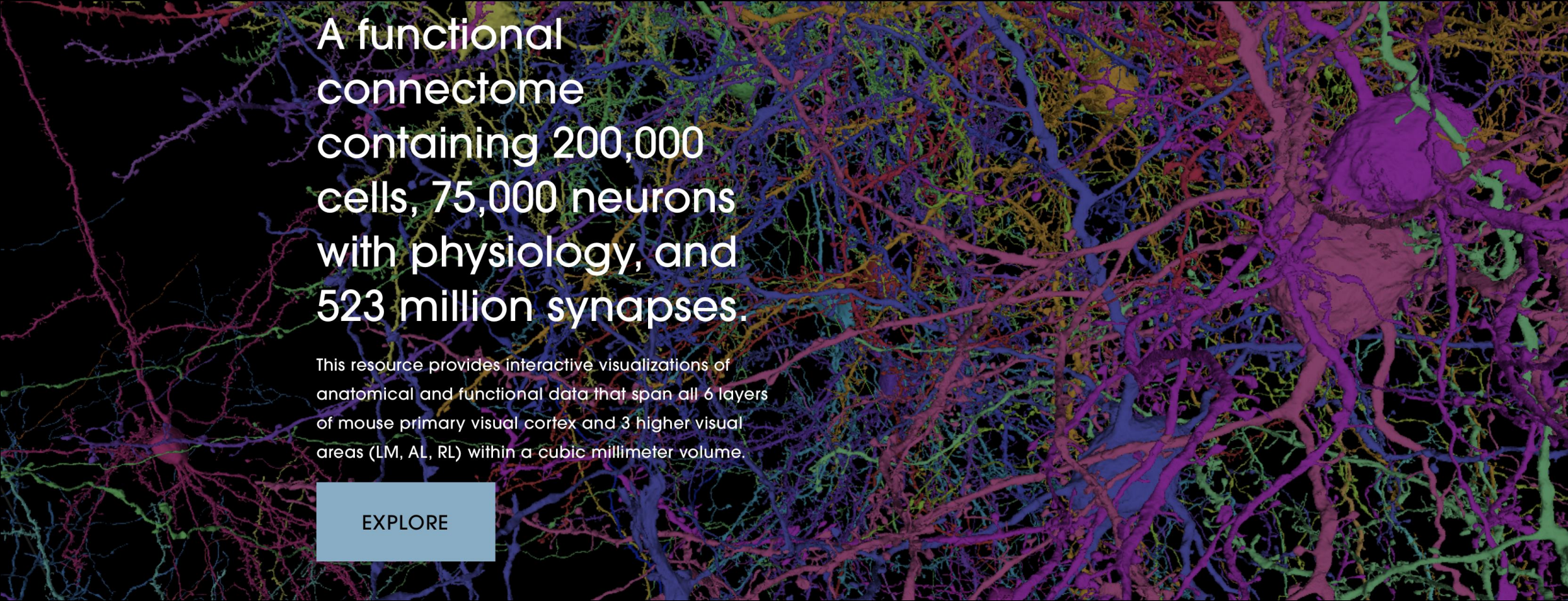
# Generalization to new neurons and mice



Median  $CC_{norm}$  on Testing Stimuli







A functional  
connectome  
containing 200,000  
cells, 75,000 neurons  
with physiology, and  
523 million synapses.

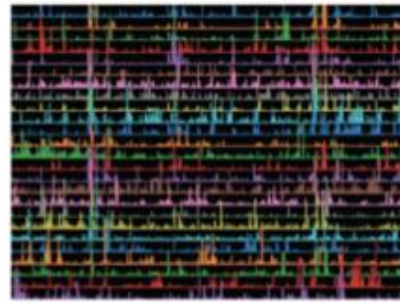
This resource provides interactive visualizations of anatomical and functional data that span all 6 layers of mouse primary visual cortex and 3 higher visual areas (LM, AL, RL) within a cubic millimeter volume.

EXPLORE

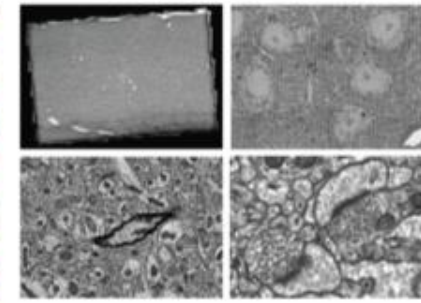


# Data Types

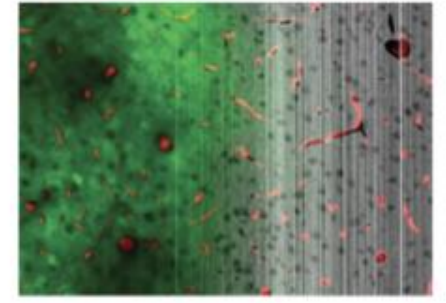
Available as a resource



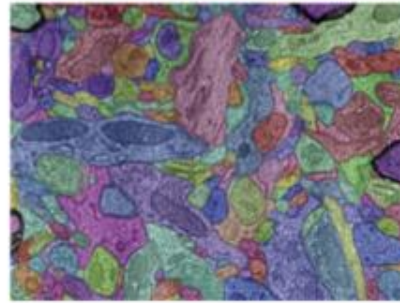
FUNCTIONAL DATA



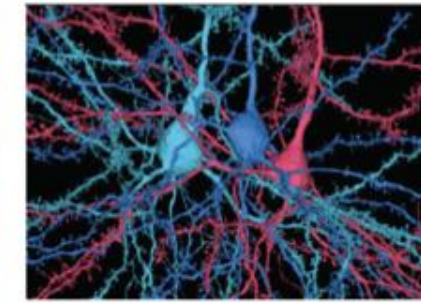
ELECTRON MICROSCOPY  
IMAGERY



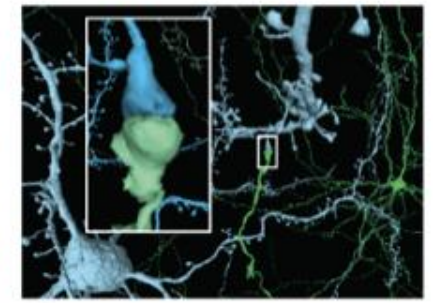
FUNCTIONAL -STRUCTURAL  
CO-REGISTRATION



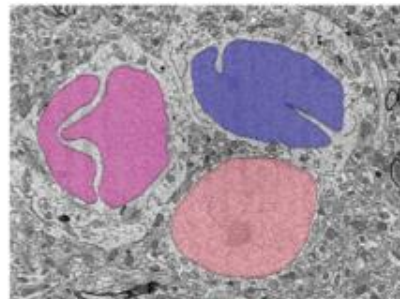
CELL SEGMENTATION



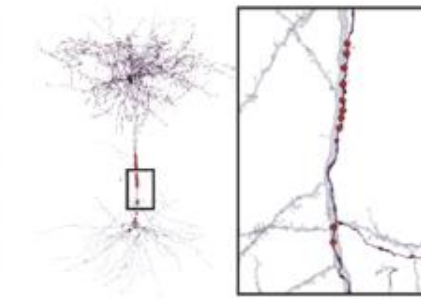
CELL MESHES



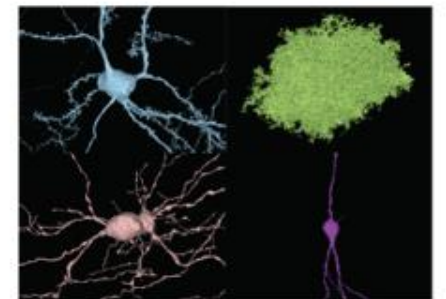
SYNAPSE CONNECTIVITY



NUCLEUS  
SEGMENTATION



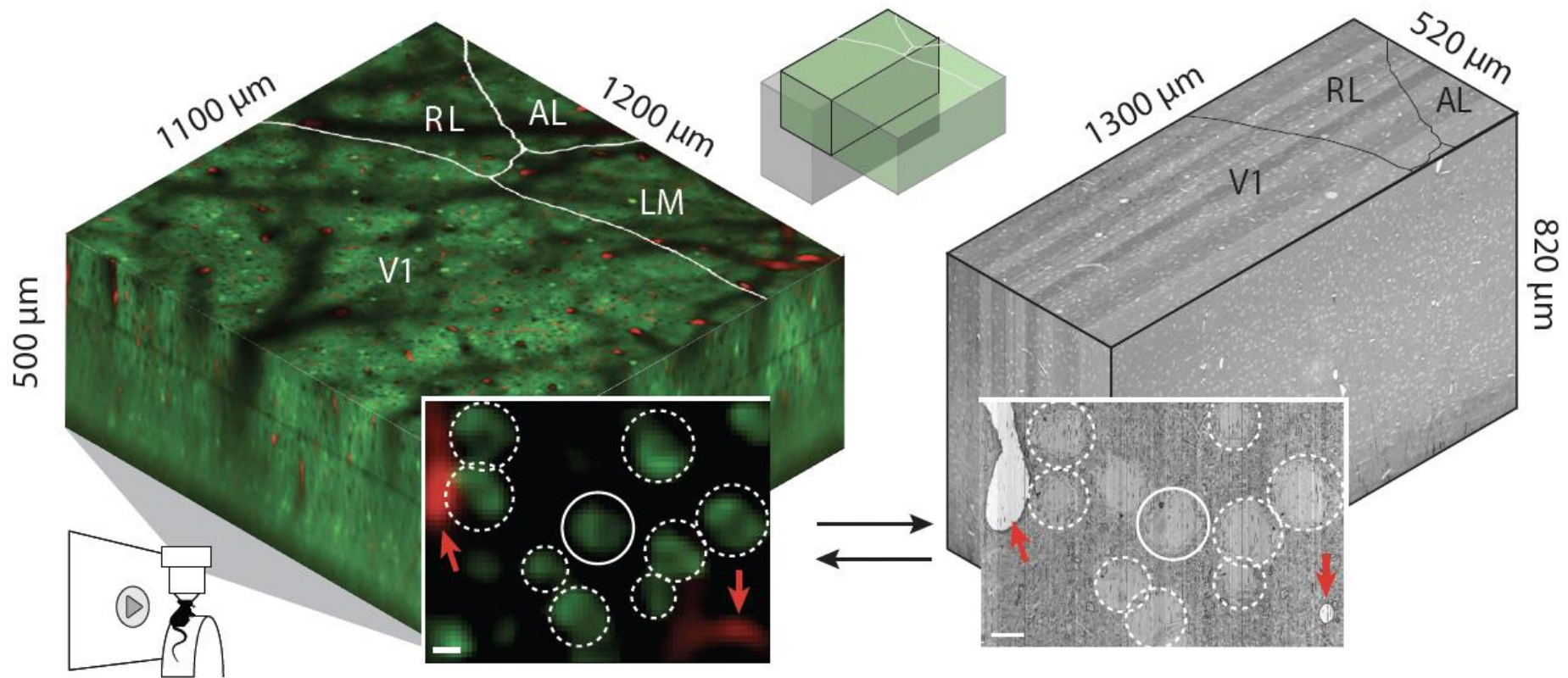
PROOFREADING  
STATUS



CELL TYPES

Slide courtesy of Prof. Andreas Tolias

Bae et al., Nature 2025



- mesoscopic 2-photon calcium imaging

- large scale high resolution  
electron microscopy



Zhuokun  
Ding



Paul  
Fahey



Stelios  
Papadopoulos

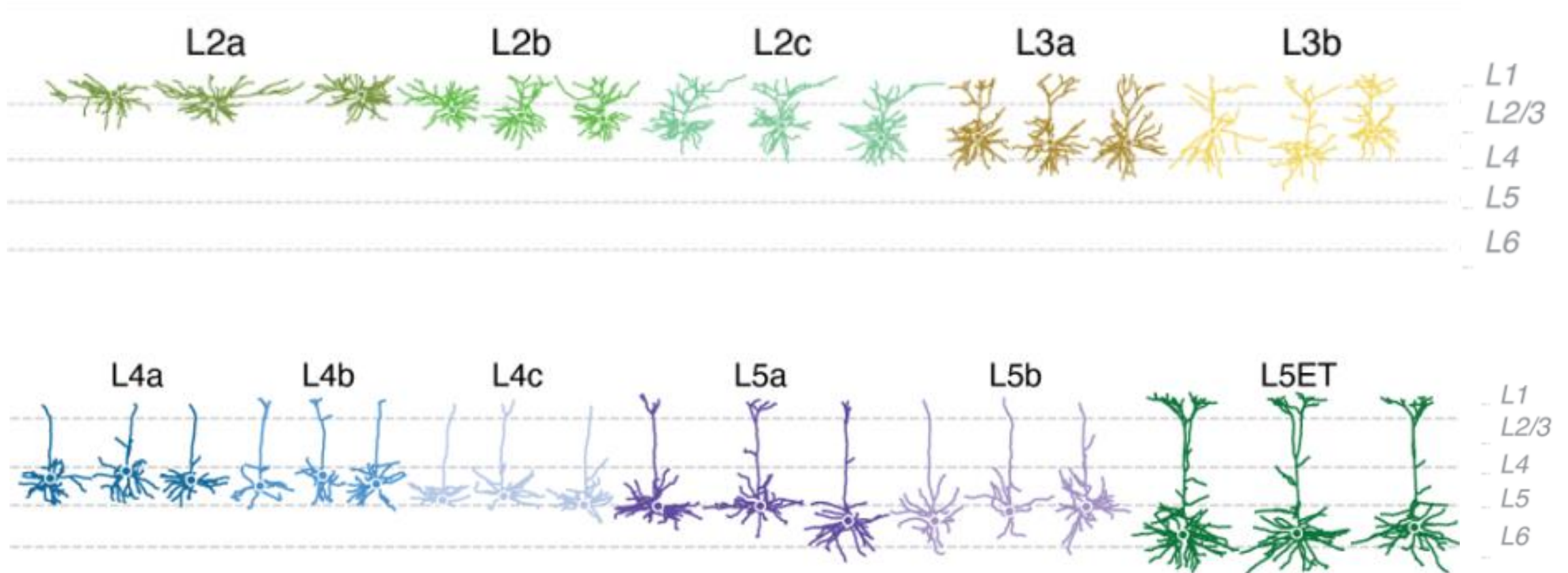


Andreas  
Tolias

Ding, Fahey, Papadopoulos et al., Nature 2025

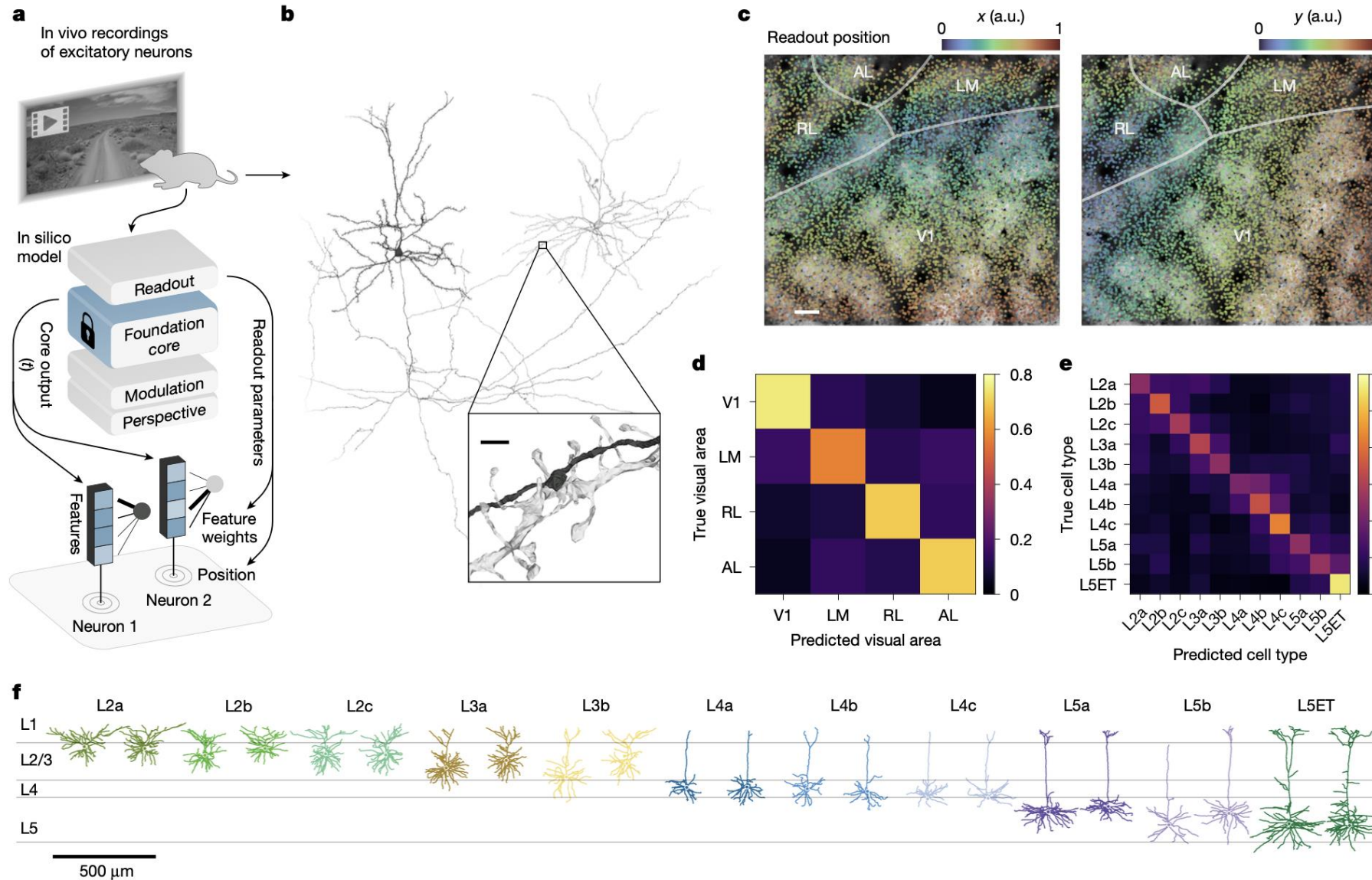


# Predict morphological cell types in MICrONS data





# Predict morphological cell types in MICrONS data



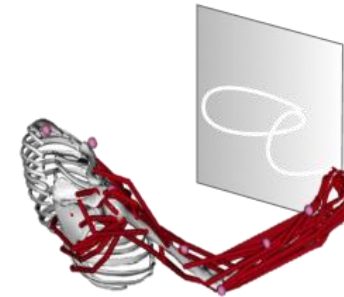
- They could recover the retinotopic map! (c)
- **AREA PREDICTION:** readout weights could predict visual areas with a balanced accuracy of 68%, exceeding the chance level of 25% (d)
- **CELL TYPE:** Using logistic regression they achieved a balanced accuracy of 32% for cell-type prediction, outperforming the chance baseline of 9% (e)

# Task-driven modelling

Yamins et al. PNAS 2014, Sussillo et al. 2015 Nat Neuro, Kell et al. 2018 Neuron, Banino et al. 2018 Nature ....

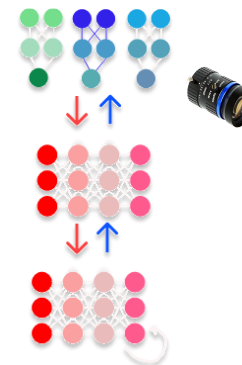
**how task-driven models  
can inform us about the  
computational goals of  
the brain**

***(which can lead to  
validations and/or new  
ideas for AI)***

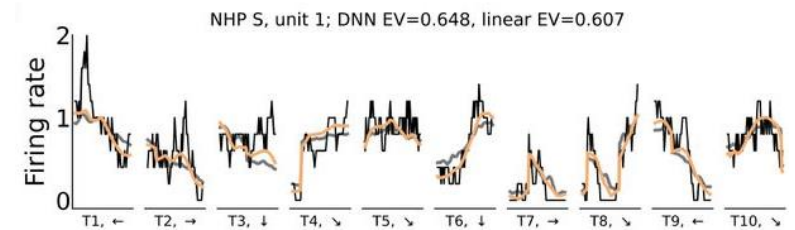


Constrain ANN based on  
behavioral task to test  
hypotheses about a system

Sandbrink et al. 2023 eLife



**Data**  
**Task-driven models (hand position and velocity task)**  
**Linear model**

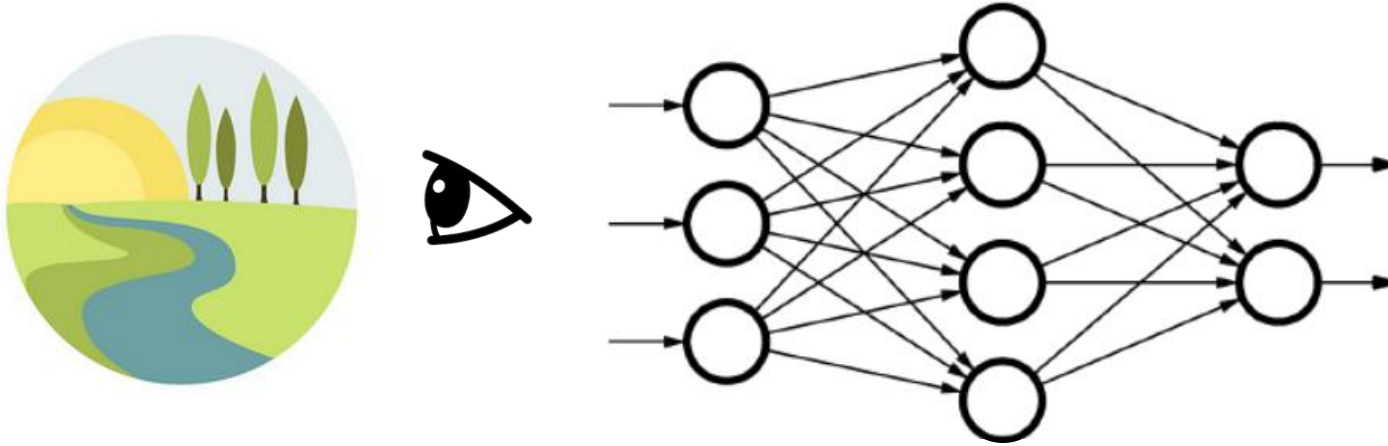


NHP S, unit 1; DNN EV=0.648, linear EV=0.607

Marin Vargas et al. 2024 Cell

NN models that describe  
neural variance & computationally  
constrain system

# Using deep neural networks as task-driven models of a system



cat



Vision: Yamins et al. (2014) .. Wang et al. (2025)



Audition: Kell et al. (2018)- speech recognition,  
speaker identification, natural sound  
identification



Barrel Cortex: Zhuang et al. (2017)



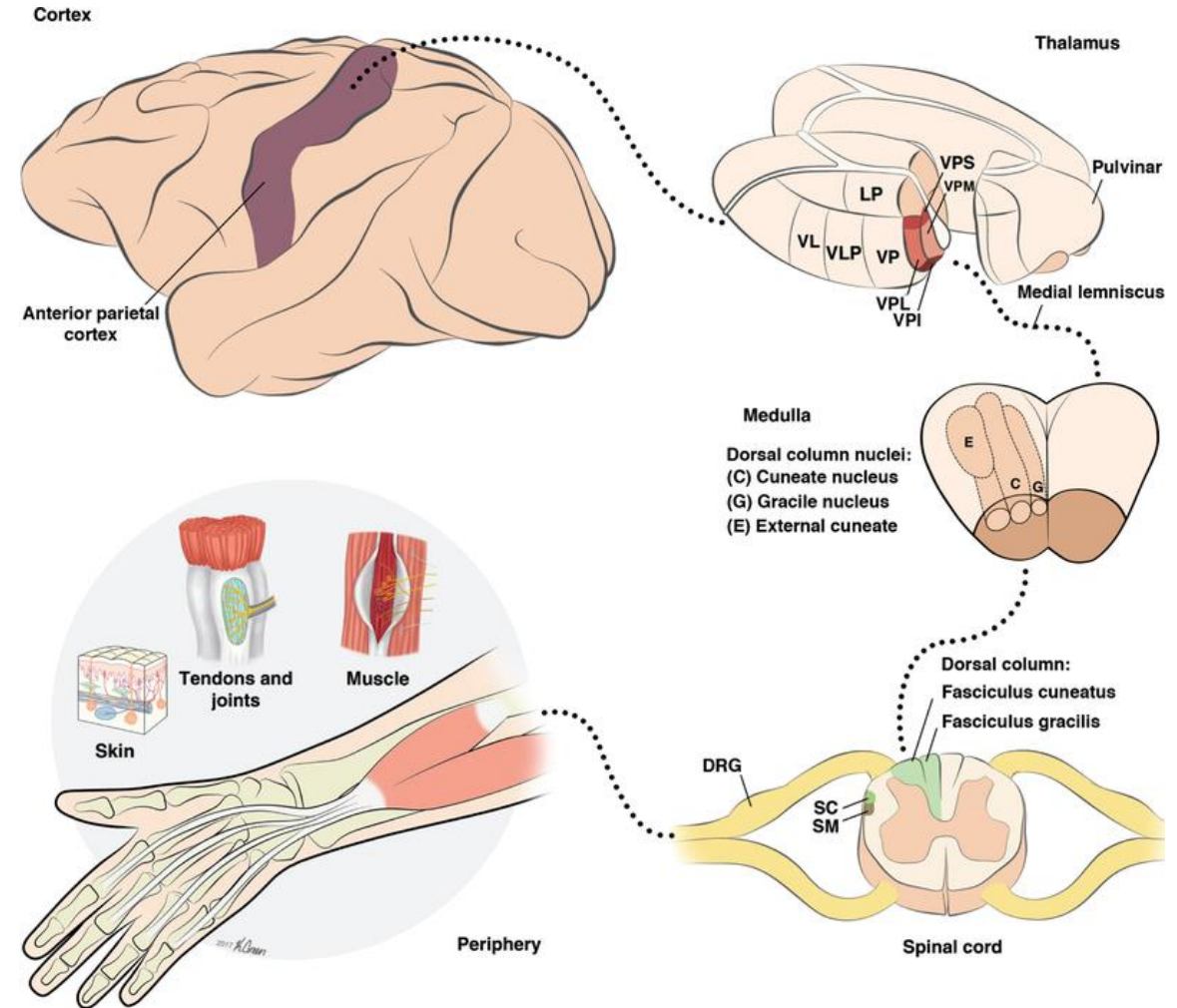
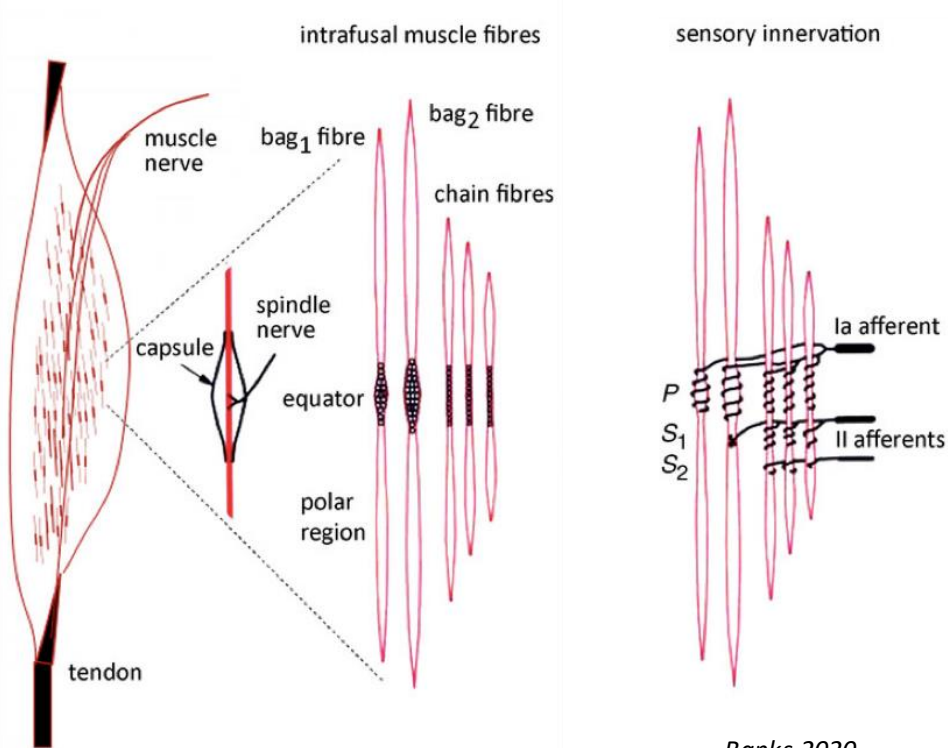
Cognition: Mante et al. (2013)



Proprioception: Sandbrink et al. (2023), Marin Vargas\*, Bisi\* et al. (2024)

# Proprioception (the sense of posture)

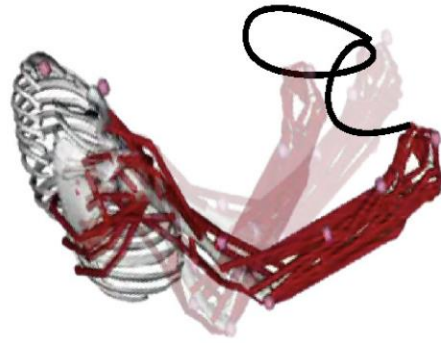
## Muscle spindle



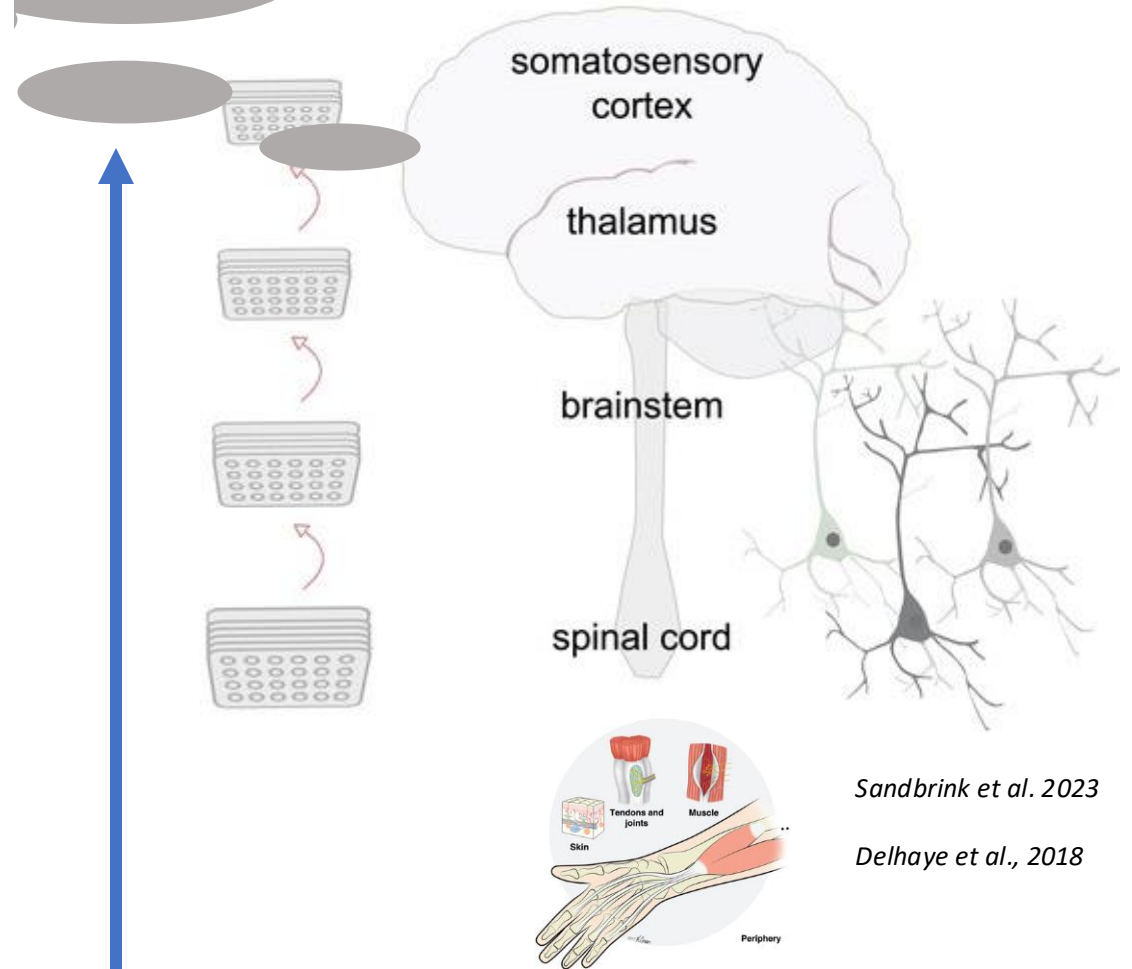
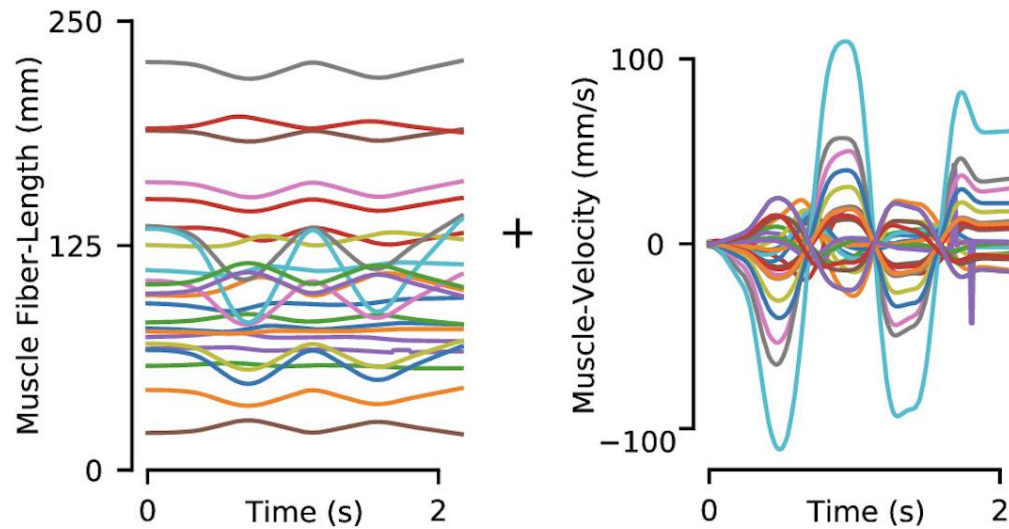
Delhaye et al., 2018



What's the trajectory of my limbs?

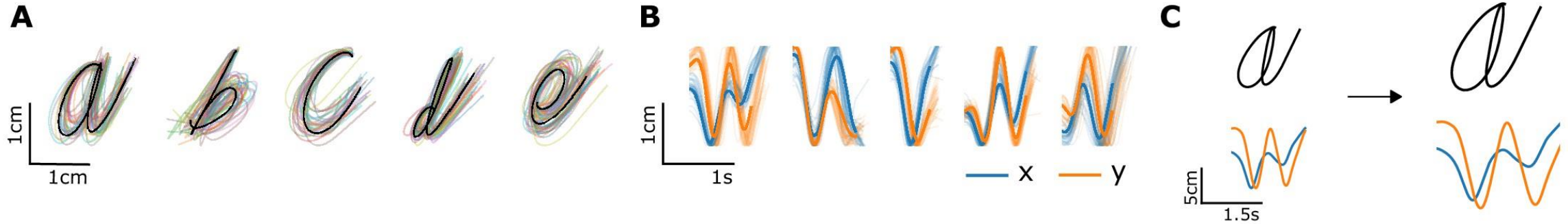


**What is the integrative logic of proprioception?**



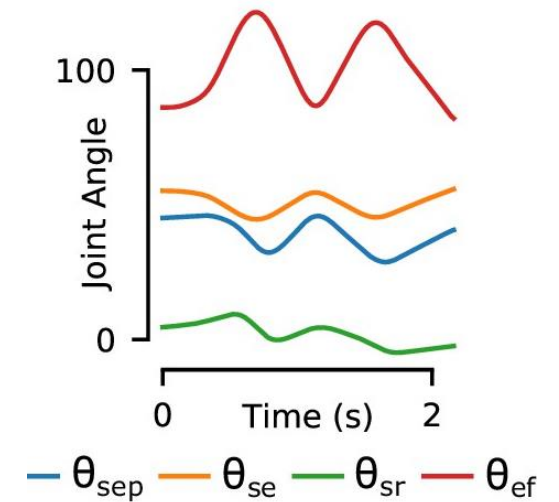
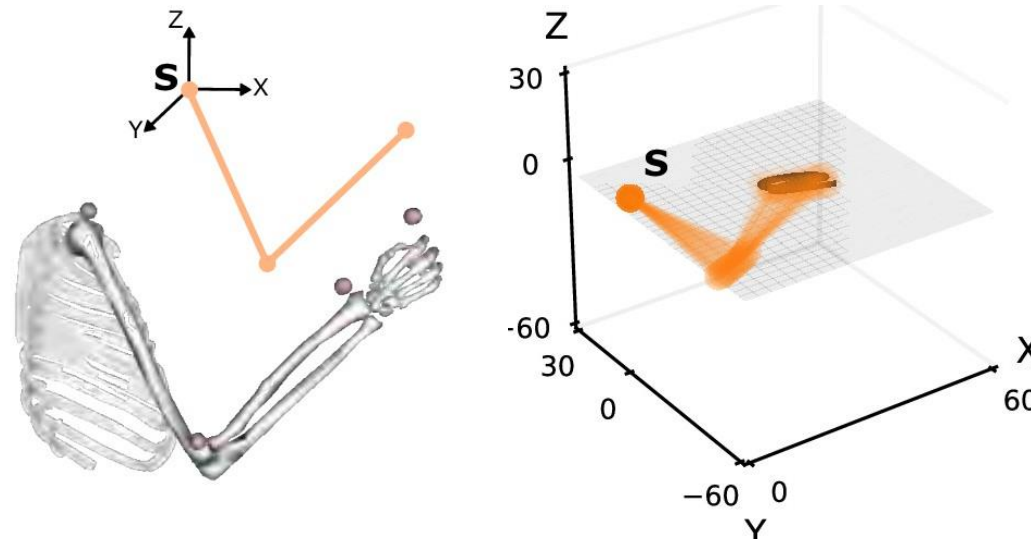


# Task development: arm movements in 3D space

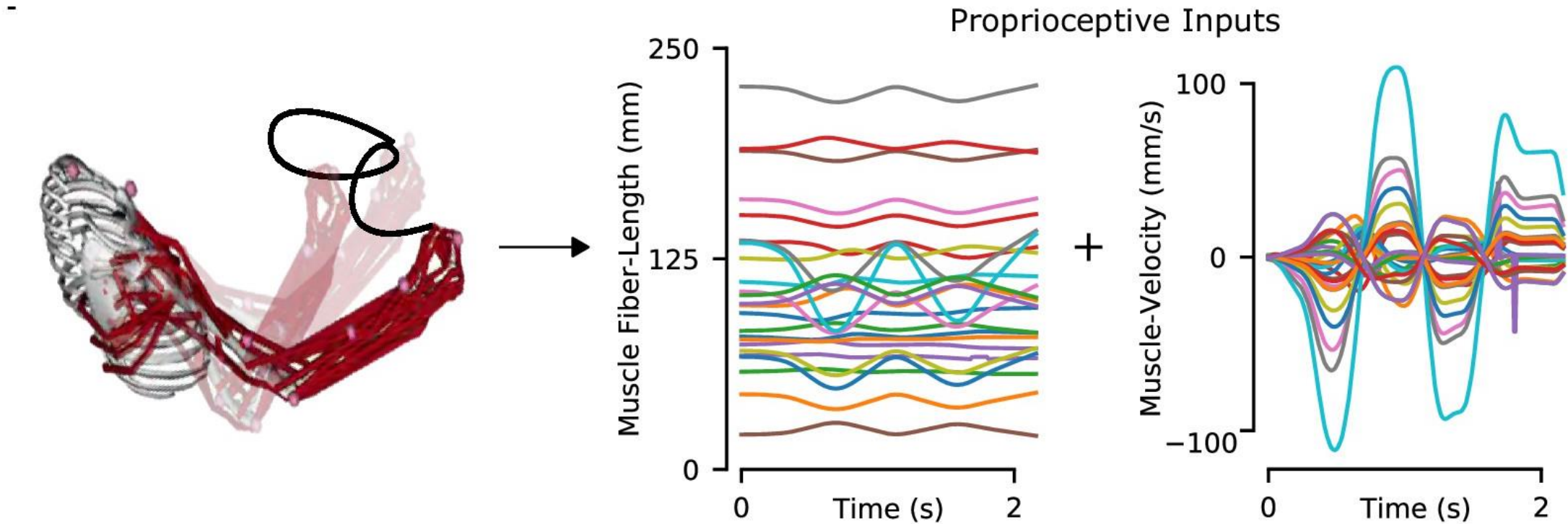


Human pen-tip  
movements writing  
Latin alphabet

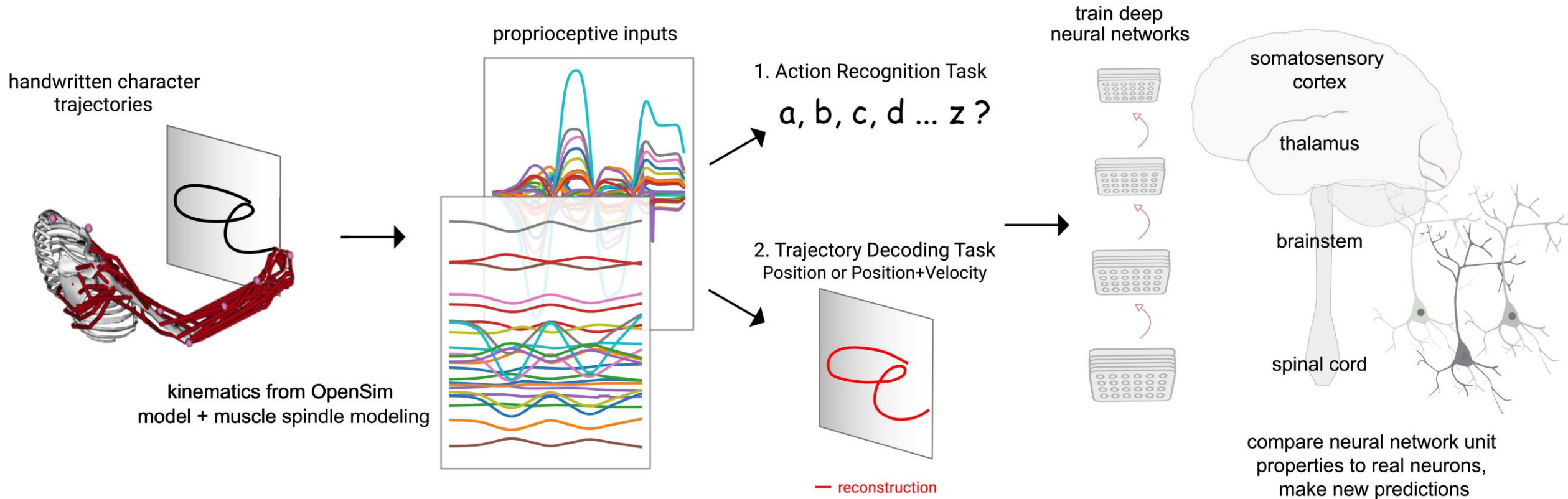
Generate synthetic arm  
trajectories to re-create  
movement in 3D space



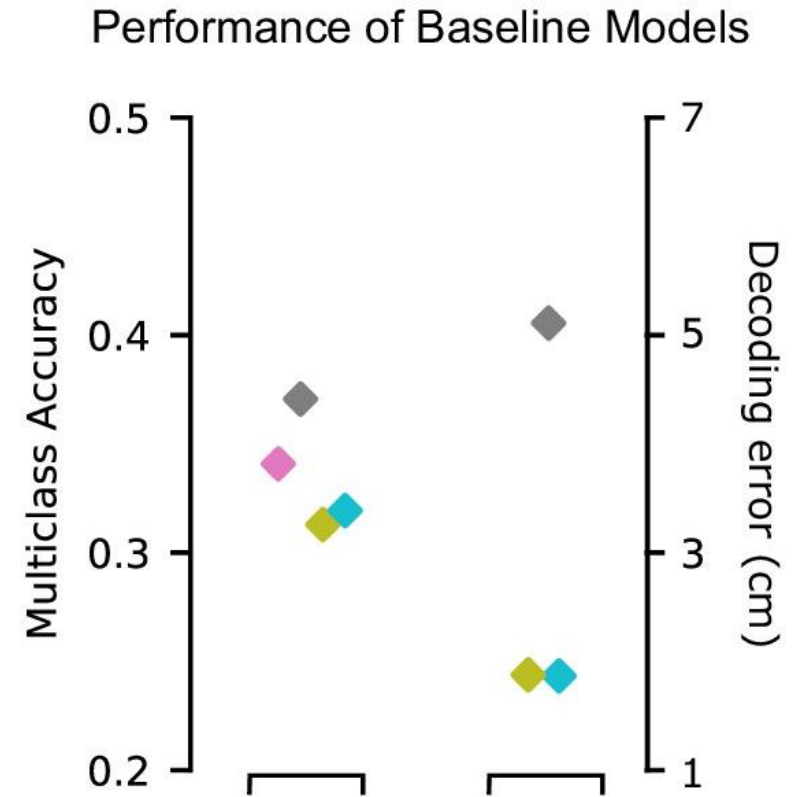
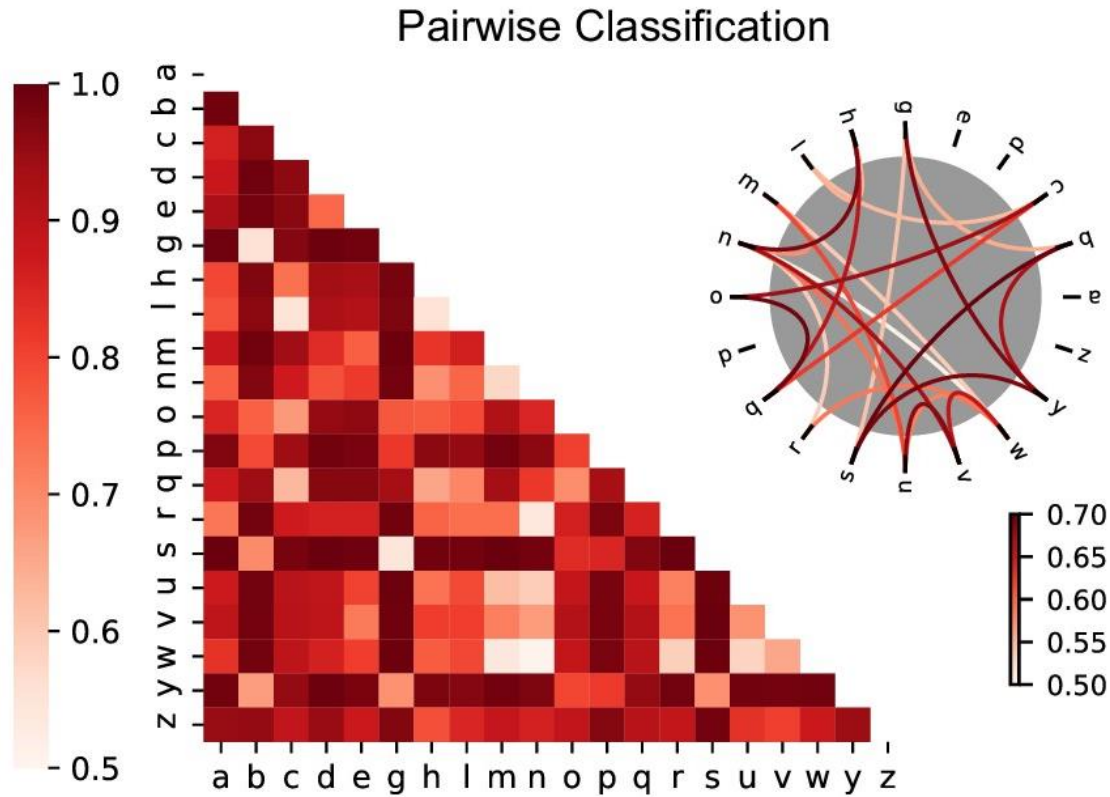
# Derive muscle spindle activity for 1M trajectories



# Task-driven modelling for the sensori(motor) system



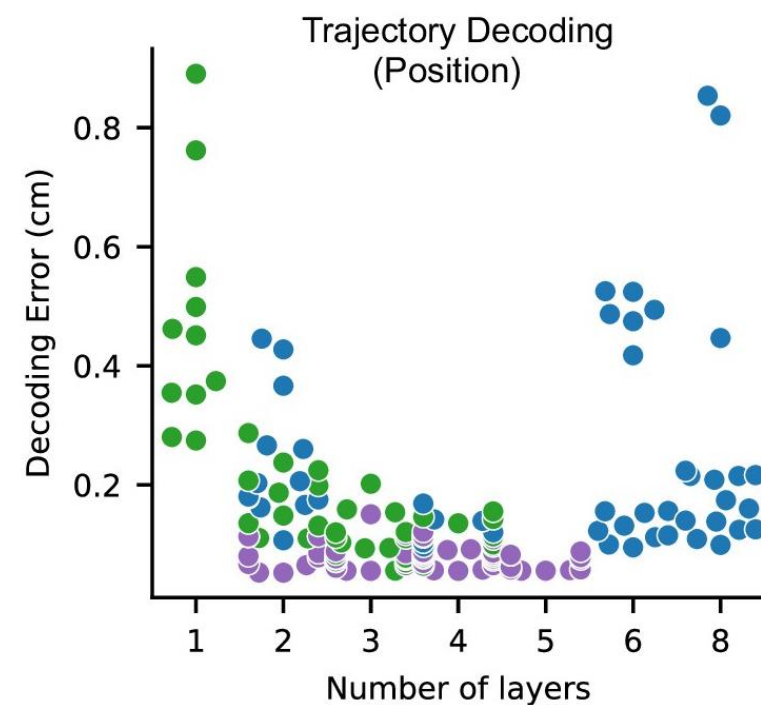
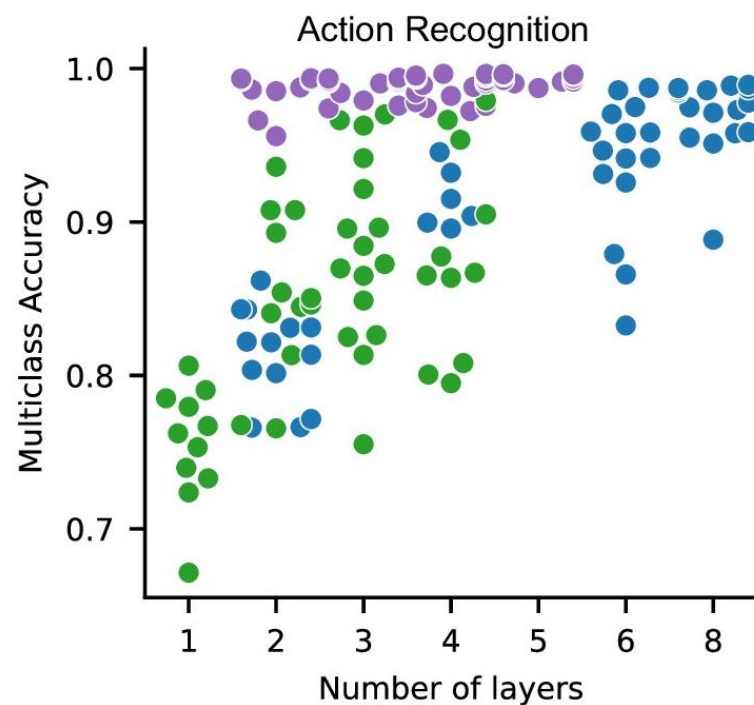
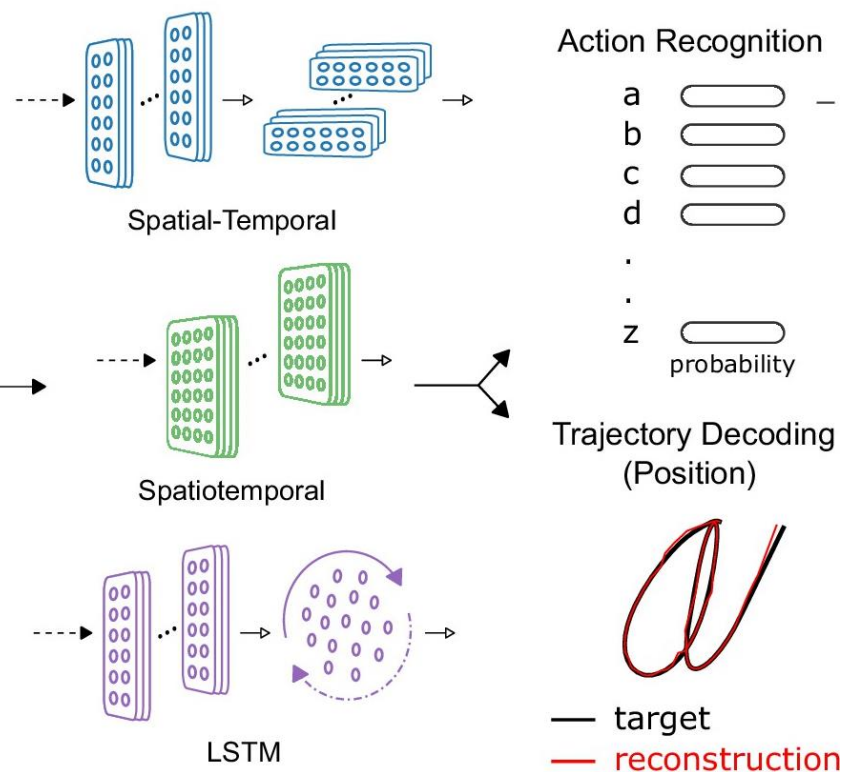
# multi-class SVMs trained on proprioceptive inputs show action recognition is a hard task



- End-effector Coords
- Proprioceptive Input
- Joint angles
- Muscle Lengths

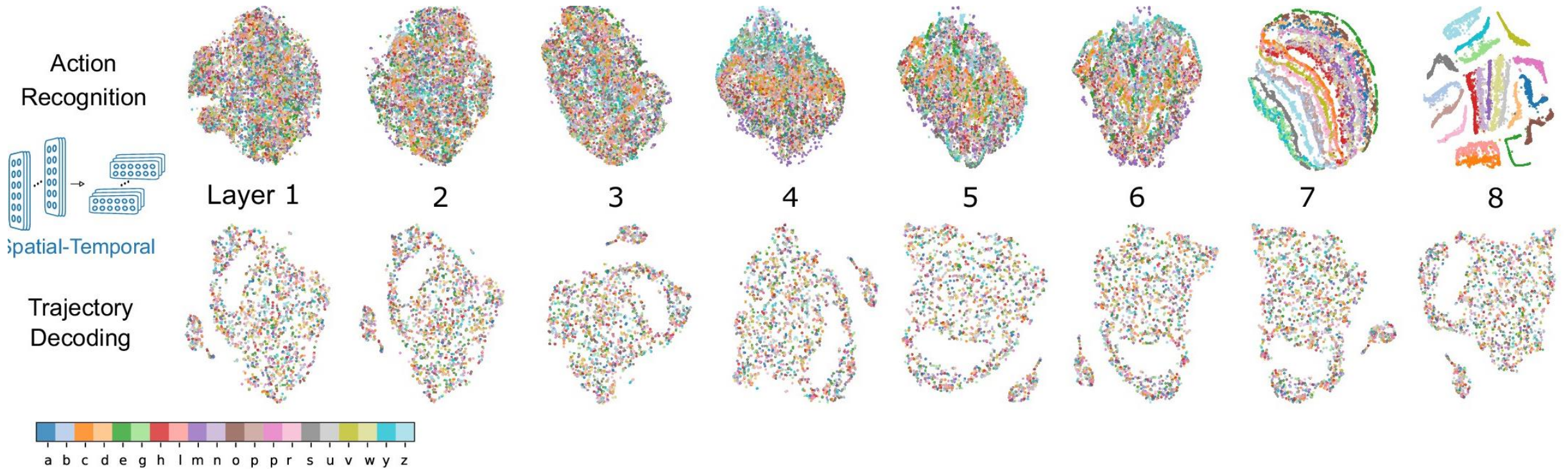


# Neural networks can readily solve both action recognition and trajectory decoding



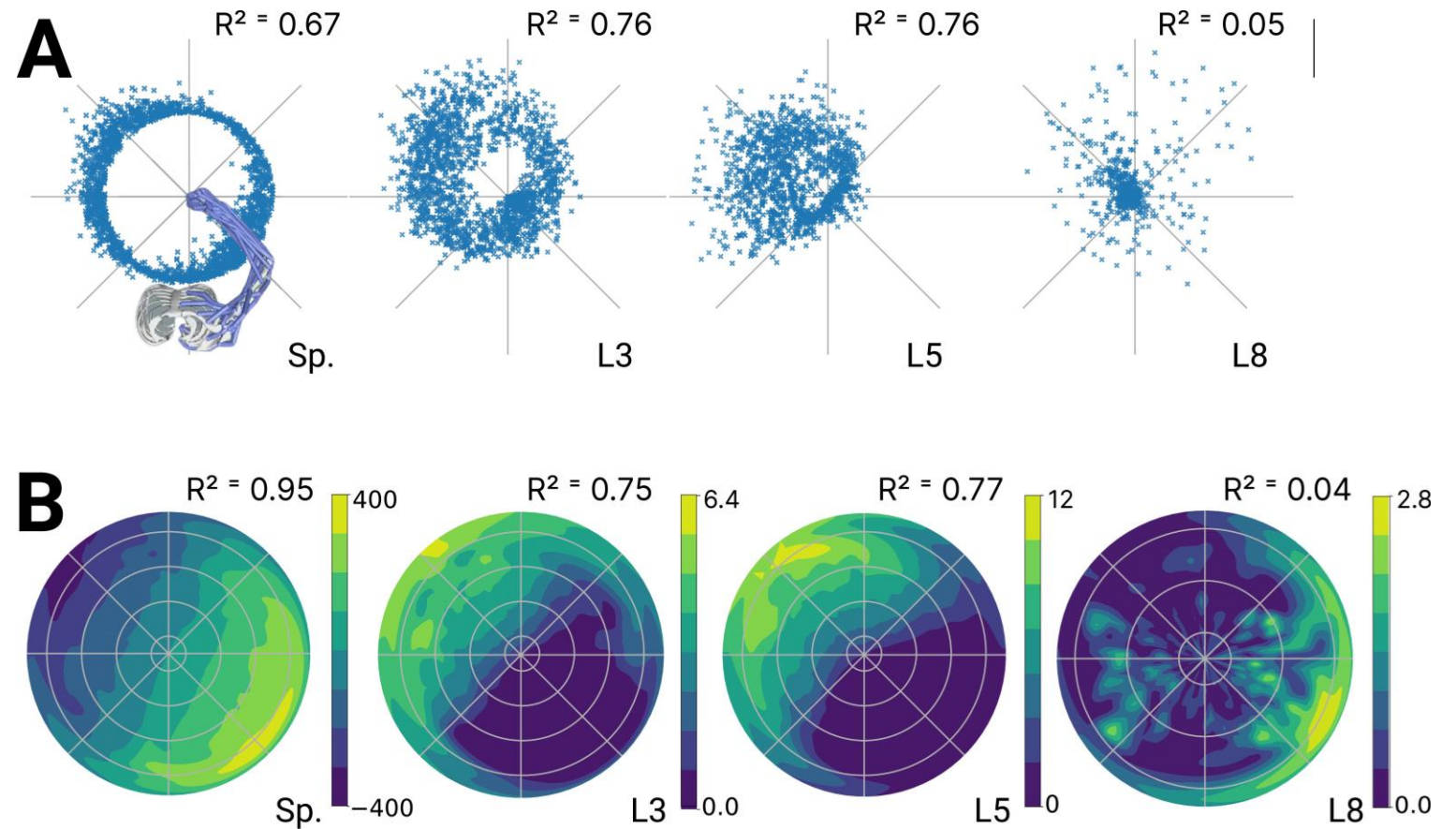
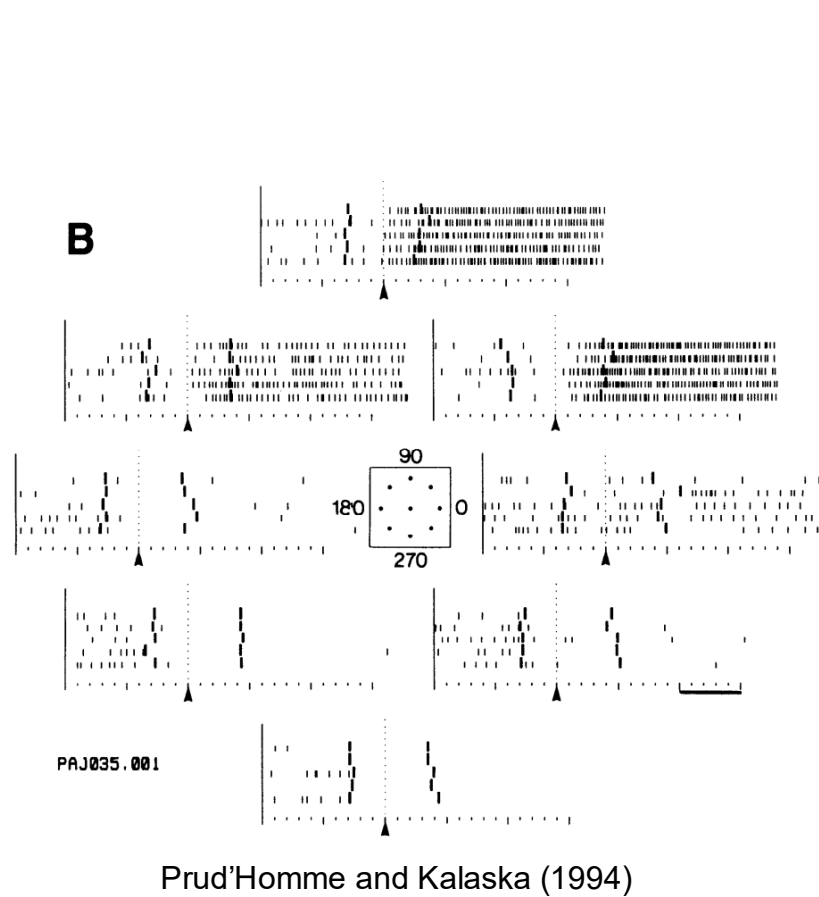


# Different representations “emerge” in NNs trained on action recognition or trajectory decoding



- Here, we used tSNE (nonlinear method) to look at changes in Label clustering across NN layers

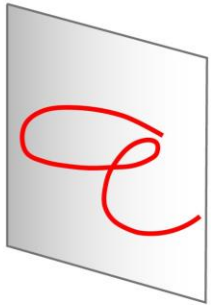
# Tuning curve analysis of NN units show canonical S1-like tuning



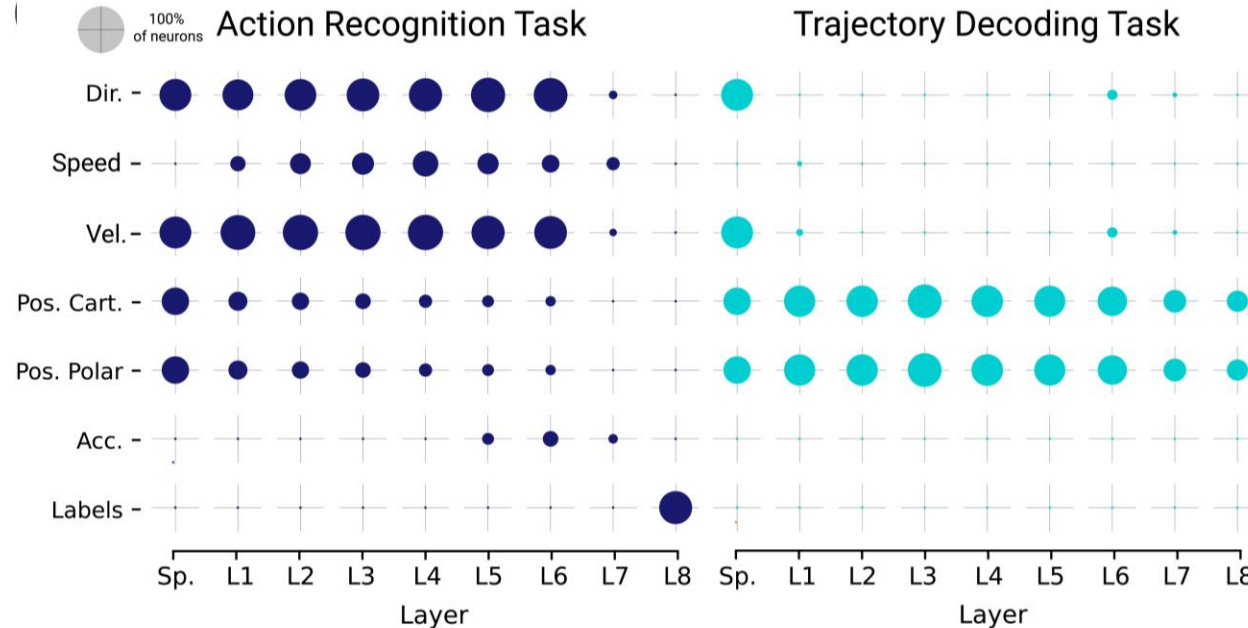
# ART-trained models contain direction selective units, but TDT-trained do not ...

1. Action Recognition Task  
a, b, c, d ... z ?

2. Trajectory Decoding Task  
Position or Position+Velocity

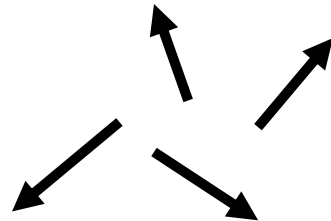


— reconstruction



Textbooks tells us:

- proprioception is there to tell us where our body is in space
- We should see direction selectivity & positional information ...
- **If we train only on ART we see direction, *less* position; traj → position and no dir .. independent of ref. framework**

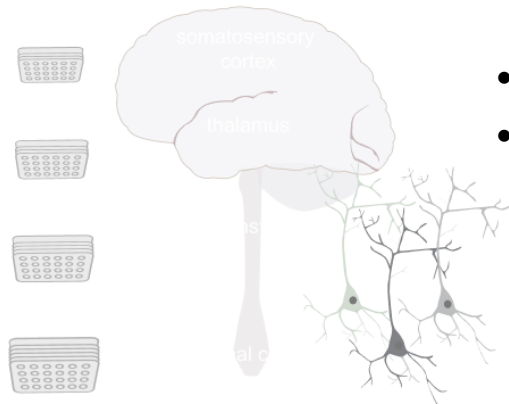
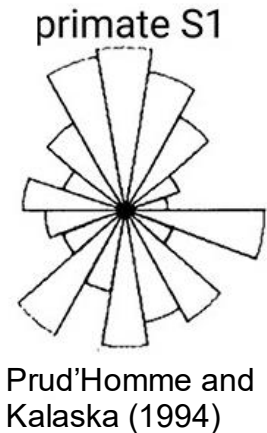




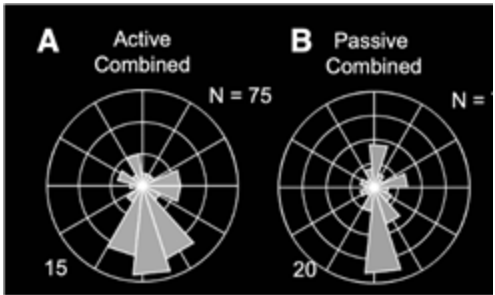
# Population vector analysis of NN units show canonical S1-like tuning, in trained models

. Action Recognition Task

a, b, c, d ... z ?

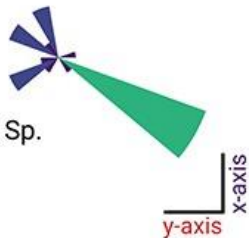


- ART Layer 4-5 most S1 like
- Hypothesized that:
  - cuneate nucleus closer to layer 1-2
  - S2 deepest layers (6+)



Versteeg et al.,  
Journal of Neurophysiology (2021)

Spindles



ART-trained



Untrained



Layer 1



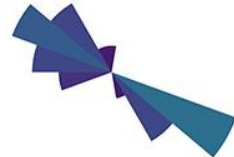
Layer 2



Layer 3



Layer 4



Layer 5



Layer 6

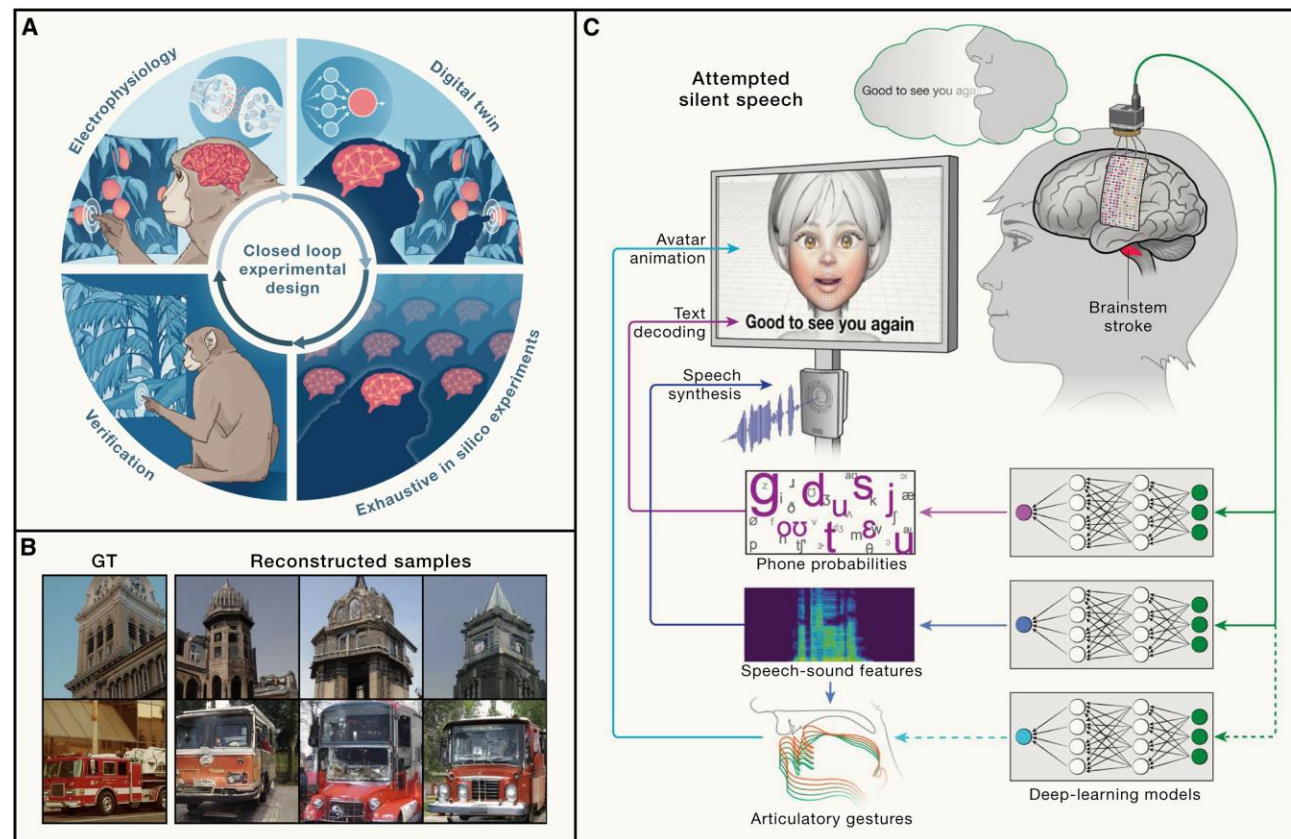
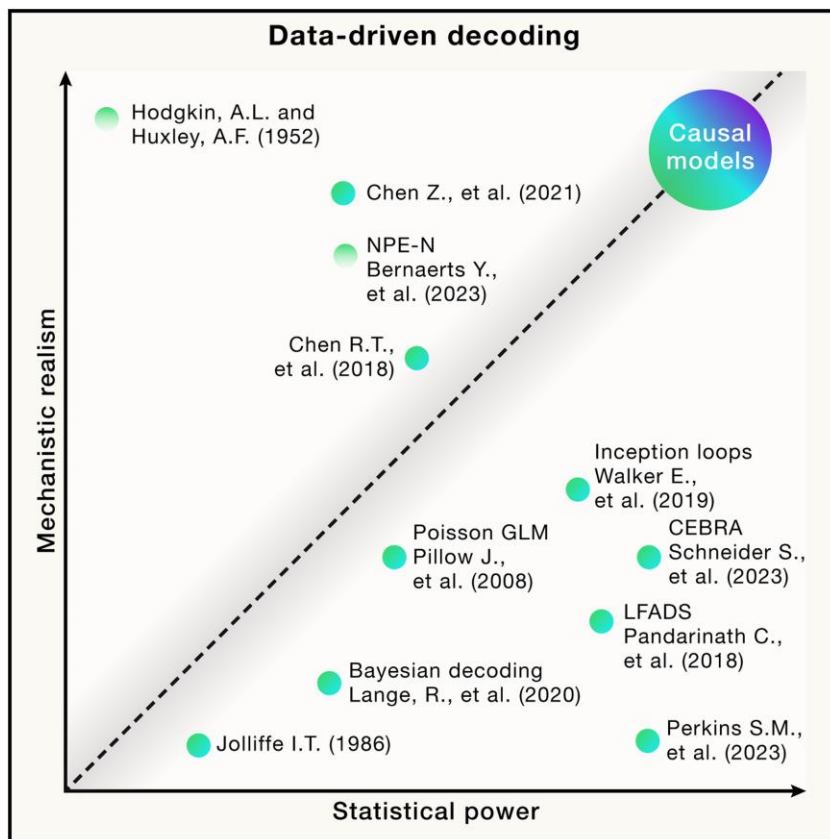


Layer 7



“Biomechanics only”  
show direction  
tuning...

# Decoding the brain: towards more causal models ...





# neuroAI in labs at EPFL:



<https://www.epfl.ch/labs/schrimpf/>

Prof. Dr. Martin Schrimpf



<https://www.mathislab.org/>

Prof. Dr. Alexander Mathis



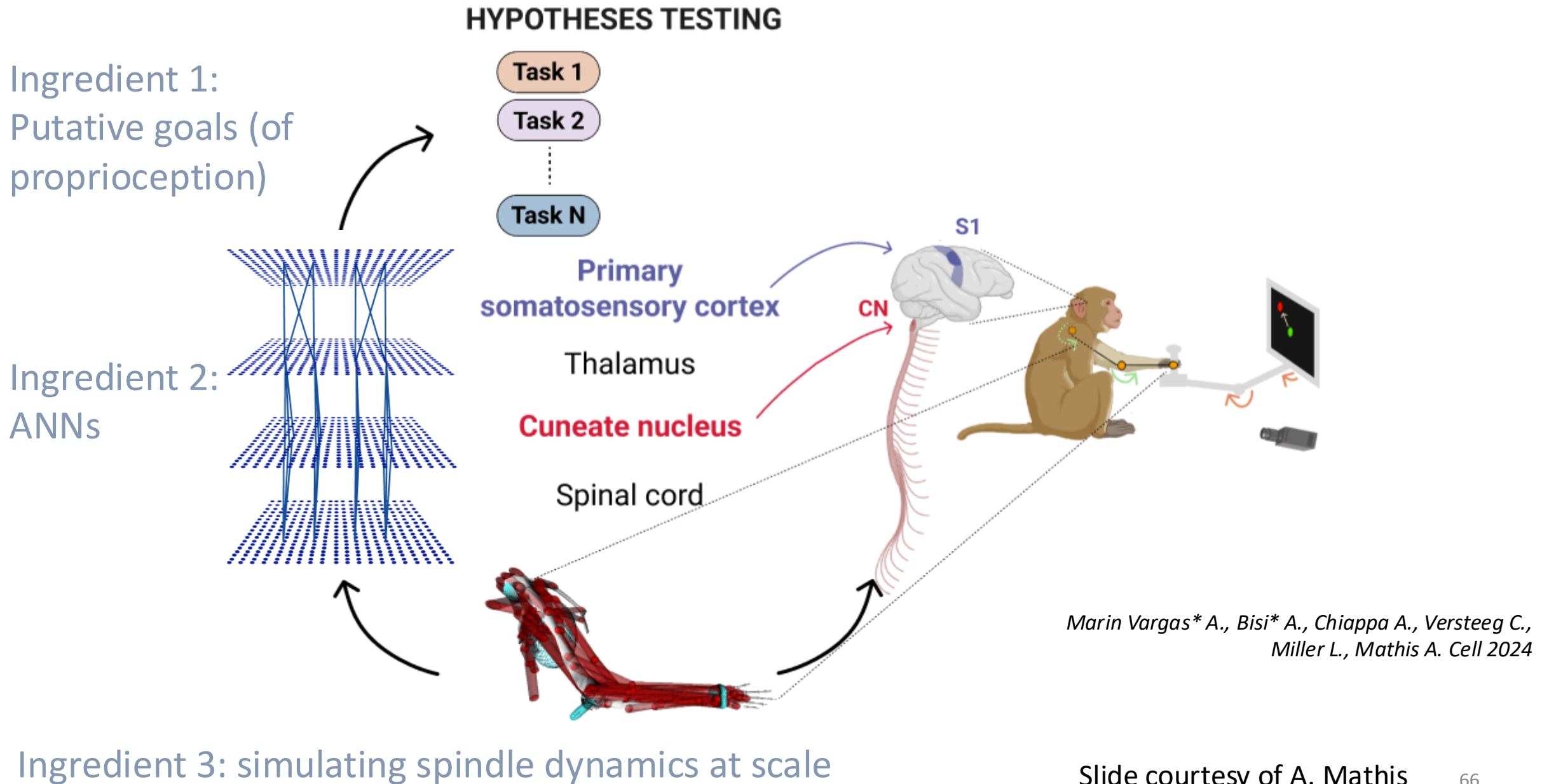
<https://www.mackenziemathislab.org/>

Prof. Dr. Mackenzie Mathis

# Summary

- NeuroAI is an emerging discipline that crosses across systems neuroscience and computer science
- It's goal is broadly to use neuro insights to build AI, and to develop AI for understanding the brain (neuro)
- It is needed as it is still VERY hard to develop embodied AI, human-like movement into robotics, and we still lack generally intelligent systems (although LLMs for language are impressive ... )
- Key example in Neuroscience inspiring AI: convolutional neural networks (likely transformers too “attention”): this is a hot area in industry – using cognitive neuro approaches to study NN btw!
  - Interestingly, CNNs developed representations similar to the brain
- Key examples of AI influencing neuro: better behavioral analysis tools, better neural analysis tools (see also BCI week soon!)
- What is missing? NNs are very simple “neurons,” that lack the complexity of what we find in the real brain: an opportunity awaits!
- Yet, there is a universality of the representations ...
- Data-driven and task-driven modeling: key approaches in neuroAI
- How do we model sensory systems: examples in vision and proprioception
  - What to consider: both how close they are at single cell, task performance, and population level similarity
  - Ongoing efforts: Brain-Score, **Inception Loops ... Foundation Models** to predict function < > structure

# Creating \*even more\* task-driven models of proprioception



# 16 computational tasks to create candidate models

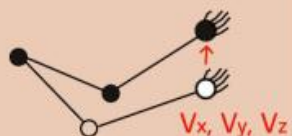
## SUPERVISED TASKS

### EgoHand hypothesis

Hand position



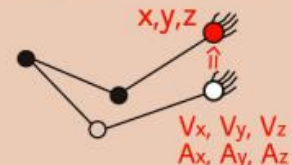
Hand velocity



Hand pos. & vel.



Hand pos., vel. & acc.



### EgoLimb hypothesis

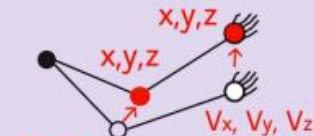
Limb position



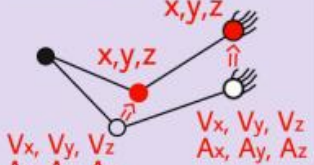
Limb velocity



Limb pos. & vel.



Limb pos., vel. & acc.

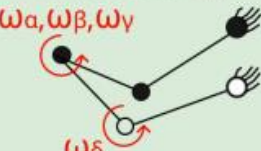


### JointLimb hypothesis

Joints position



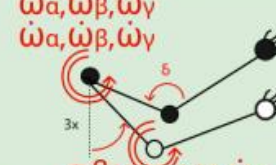
Joints velocity



Joints pos. & vel.

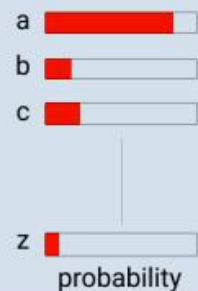


Joints pos., vel. & acc.



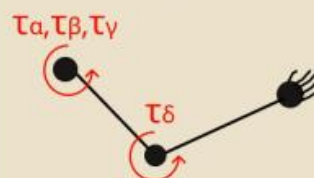
### Action recognition hypothesis

Action recognition



### Sensorimotor hypothesis

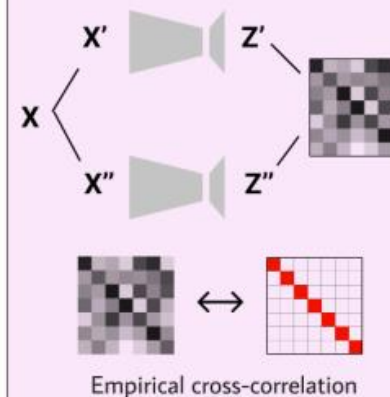
Torque



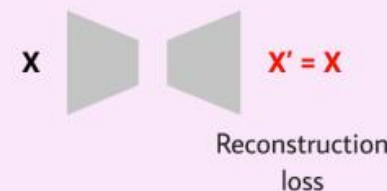
## UNSUPERVISED TASKS

### Efficient coding hypothesis

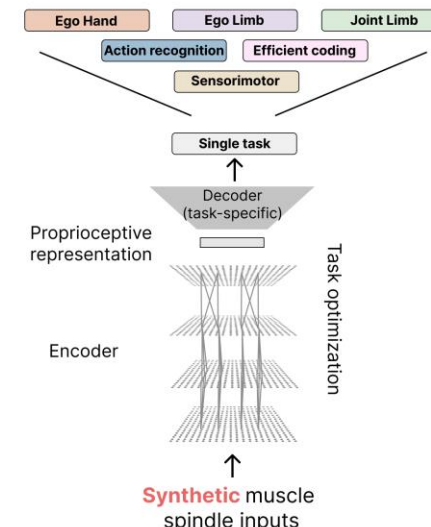
Redundancy reduction



Autoencoder



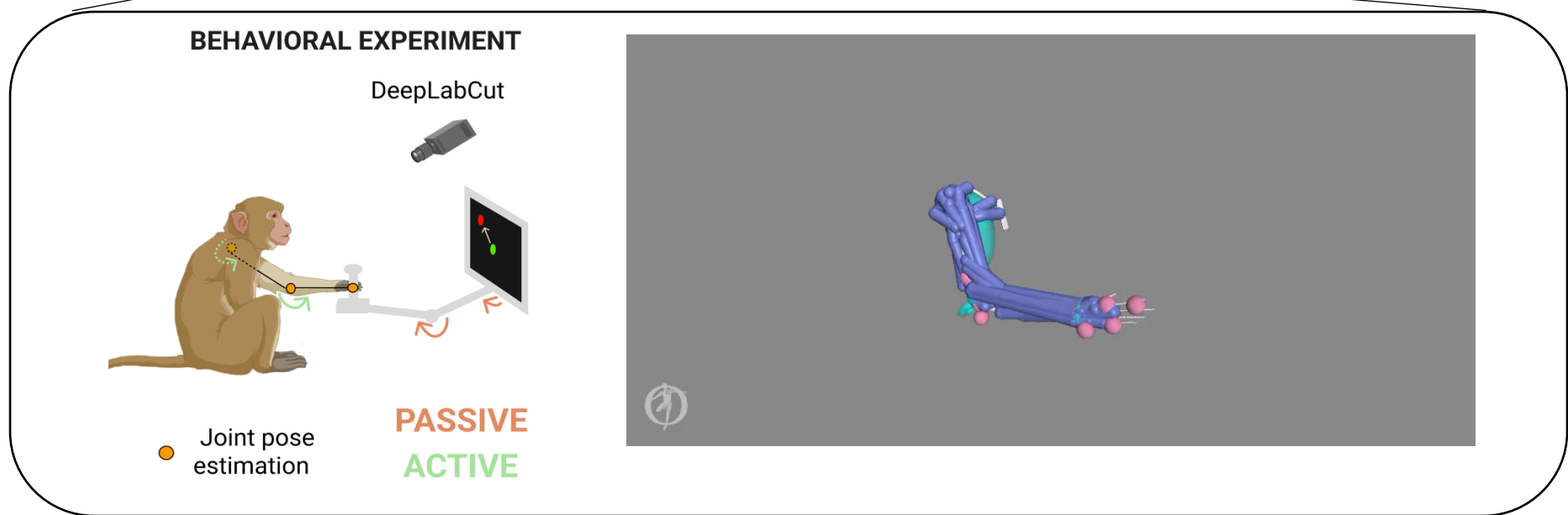
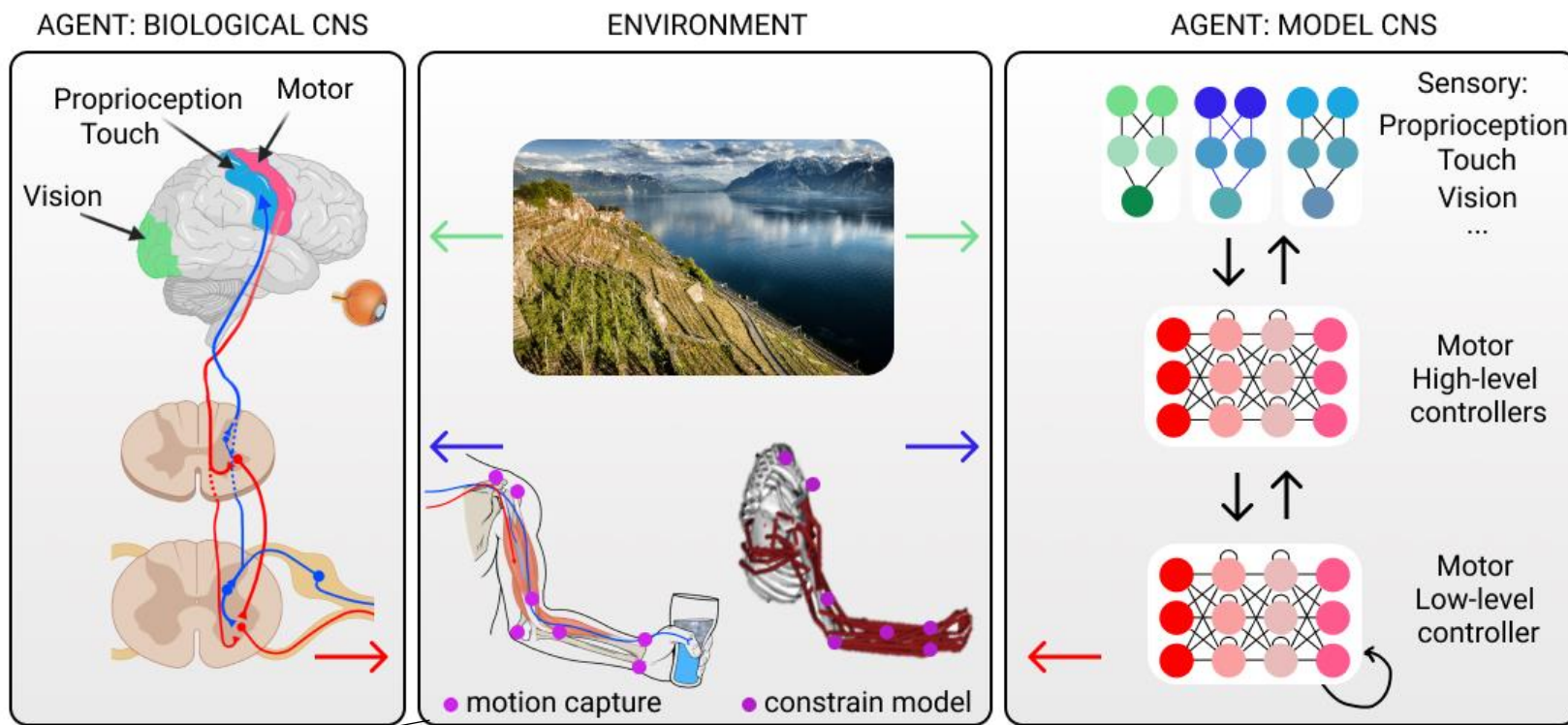
## HYPOTHESES GENERATION



Egocentric coordinates

Joints coordinates





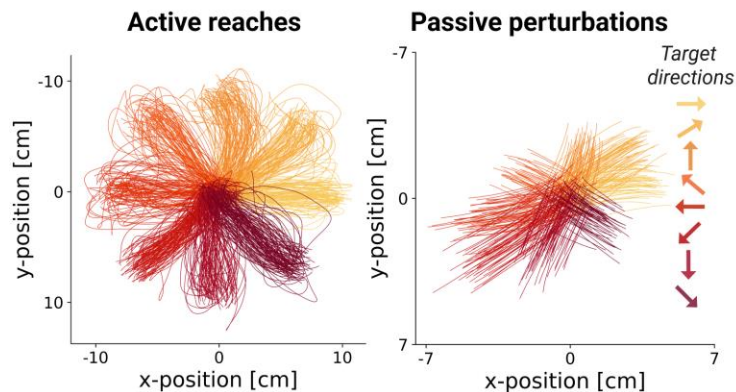
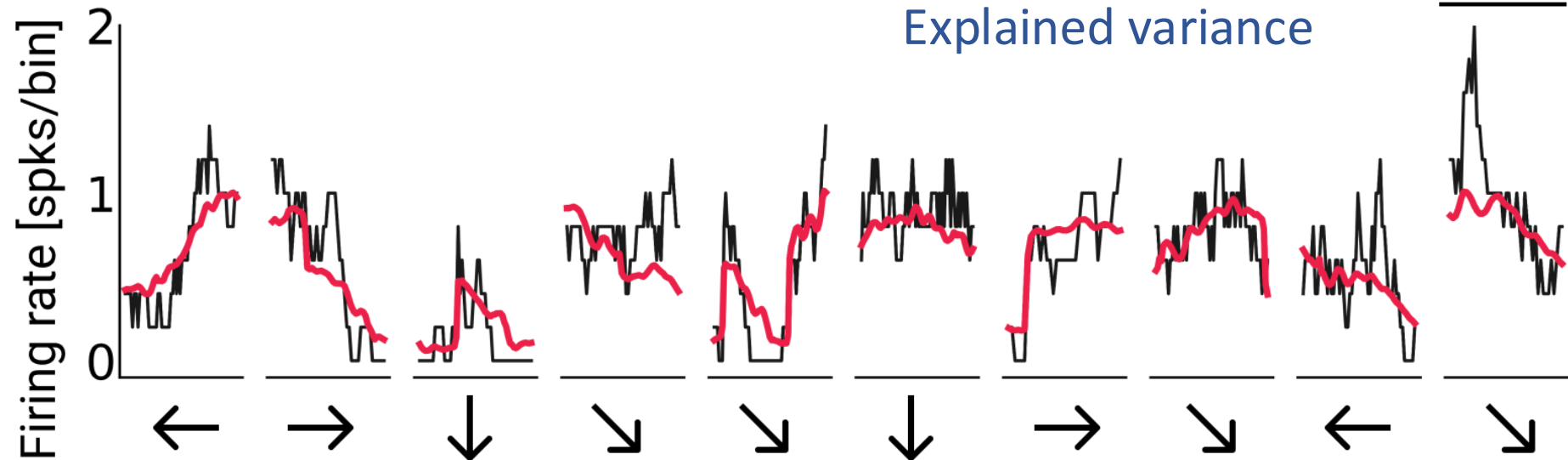
# Task-trained models predict single neuron dynamics!

Active trials

NHP S, CN unit 1 (EV=0.622)

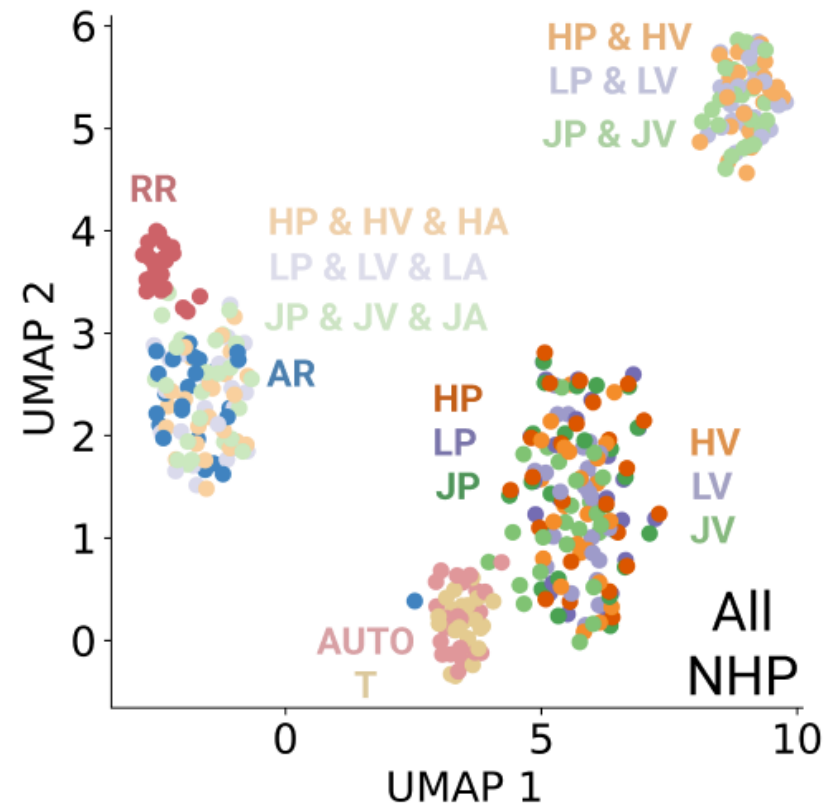
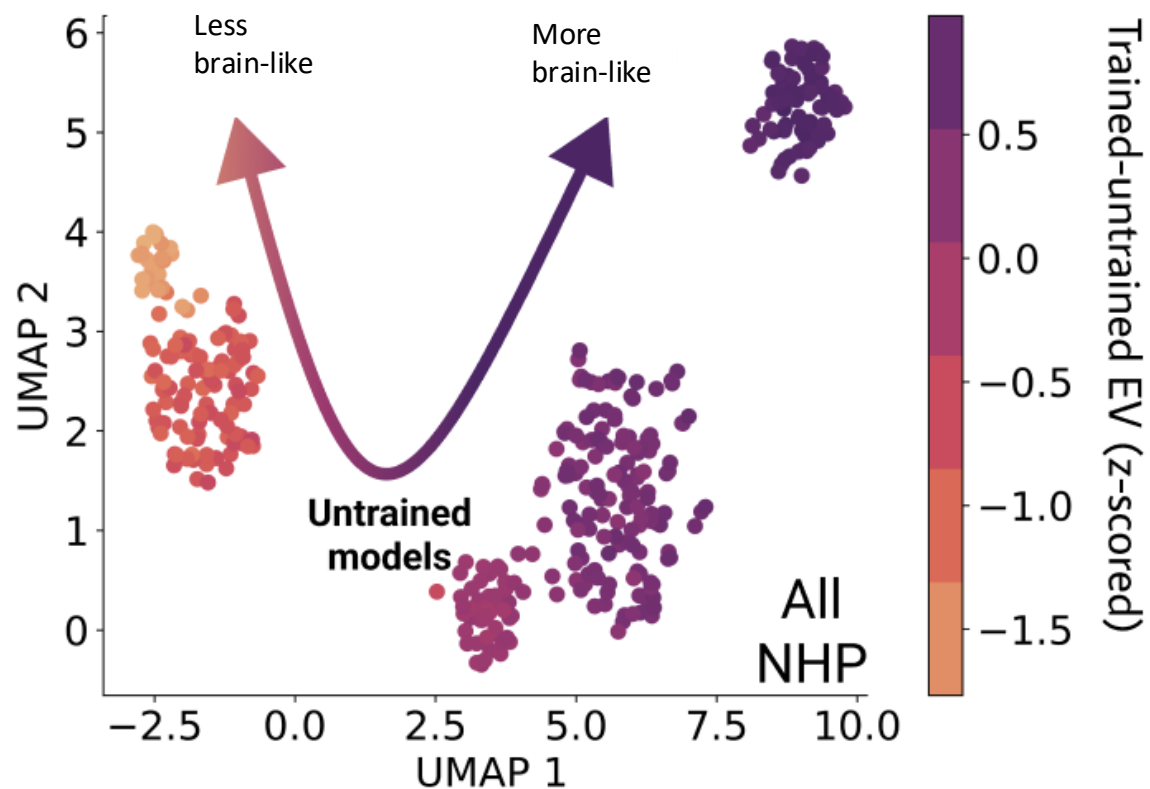
Explained variance

500 ms



# Comparing network representations with unsupervised UMAP clustering

ACTIVE



HP = Hand position    LP = Limb position    JP = Joint position  
HV = Hand velocity    LV = Limb velocity    JM = Joint velocity  
HA = Hand acceleration    LA = Limb acceleration    JA = Joint acceleration

RR = Redundancy Reduction    AR = Action Recognition  
AUTO = Autoencoder    T = Torque

# Task-trained models predict neuron dynamics!

- For all 16 hypotheses, if a *computation* is better learned on synthetic, passive spindle data, then the model also generalizes better to neural data
- Neural data (*in the active case*) is best explained by the **hypothesis that proprioception is optimized to encode the location and velocity of the body** (irrespective of coordinate framework (hand or limb))
- Lack of evidence for hierarchical processing; this suggests that proprioception even in the brain stem is dominated by efference copies ...

